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STUDIES ON SOME PROTOZOAN PARASITES OF FISHES OF ILLINOIS

WITH EIGHT PLATES

BY

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INTRODUCTION AND ACKNOWLEDGMENT

This paper is divided into two parts. The first part deals with a preliminary observation made by the author from August 12 to September 11, 1930, under the auspices of the Illinois State Natural History Survey, on some parasitic Protozoa of fishes inhabiting the main water systems of the state. The second part gives the descriptions of several new species and additional information on a few already known species of Myxosporidia observed during this survey and also in the fishes which have been collected by Dr. D. H. Thompson, Zoologist of the Survey, from various parts of the state in connection with his work over a period of several years.

The author is indebted to Dr. Thompson for these materials placed at his disposal and for assistance during the month of field study. Thanks are also due to Mr. F. D. Hunt of the Survey, who was instrumental in the collection of material on the Fox River.

The specimens are deposited in the collections of the Illinois State Natural History Survey at Urbana.

PRELIMINARY SURVEY OF PROTOZOAN PARASITES OF FISHES OF ILLINOIS

Various protozoan parasites are known to occur in fresh-water fishes. Certain ciliates, for example, Ichthyophthirius and Cyclochaeta, if present in large numbers, have been found to become the causes of epidemic diseases in fresh-water fishes. Among Mastigophora and Sarcodina are found some species which parasitize fishes, although their effect upon the host is as a rule less noticeable. A group of Sporozoa known as Myxosporidia is, however, almost exclusively parasitic in fishes (Kudo, 1920). While numerous Myxosporidia occur in organ cavities, such as the gall bladder, urinary bladder, ureter or uriniferous tubules of the kidney, they do not ordinarily seem to exercise any harmful effects upon the body of the host. On the other hand, the Myxosporidia which attack tissues of the host produce various histopathologic changes which hinder the normal functions of the organs concerned, and appear in many cases to cause the death of the host. Death is due, not only to these protozoan parasites as the primary causes, but also to secondary bacterial or fungous infections of the affected tissues. Instances are not uncommon in which infection assumes an epidemic form and so damages the fishes that they become unmarketable or unattractive to the consumer, as in the "wormy" halibut of the Pacific coast (Davis).

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Histozoic Myxosporidia are most frequently found to attack the gills, integument, fins, muscles, etc., of fresh-water fishes, and when the infection is at an advanced stage, certain characteristic changes in the attacked tissues result. These changes are often recognizable by the unaided eye. When the viscera are affected, the myxosporidian infection as a rule is to be discovered only by dissection and microscopical examination. Even here an extreme hypertrophy of the infected tissue may, however, cause characteristic changes visible externally, as in the case of the silver-mouthed minnow infected by *Myxosoma grandis* (Figs. 1 and 2) or in the young tench suffering from a heavy infection by *Sphaerospora pernicialis* (Léger).

In the present survey the author's attention was directed mainly to tissue-attacking Protozoa, especially Myxosporidia. Each living, dead, or freshly "dressed" fish was examined first with the unaided eye with respect to external conditions, and when abnormalities were recognized, the latter were examined microscopically. If these bodily changes were found to be due to protozoans, the greater portion of the infected tissues or organs was preserved in either 4 per cent formol or Bouin's fluid for a more thorough study at the laboratory. Examination of coelozoic Protozoa was conducted only on a few occasions.

In this manner more than 1,300 fishes belonging to 35 species were examined. The fishes sold at fish markets or caught by fishermen were examined whenever possible, and in the case of the species which were not to be found in the market, seines or hook and line were used to collect them. Visiting fish markets was further useful, since general information about abnormalities or diseases of fishes in a particular locality was often obtained.

The results of the observations follow:

Polyodon spathula (paddle-fish). Fifteen fishes caught in the Mississippi River, and examined at a fish market in Davenport, Iowa, showed no histozoic protozoan infection.

Lepisosteus osseus (long-nosed gar). Six specimens examined at Dundee and Meredosia were apparently free from protozoan infection.

Amia calva (dogfish). Four fishes from the Fox River at Dundee (August 12) and two from the Illinois River at Meredosia (September 3) were examined alive and found to show no noticeable protozoan parasites.

Dorosoma cepedianum (hickory shad). Fifty-six fishes caught by seining in the Rock River near Sterling (August 19) were apparently free from histozoic protozoan infection.

Argyrosomus artedi (lake herring). About 100 "dressed" fishes examined at a fish market in Waukegan (August 14) were free from any

noticeable protozoan infection. The same was true of some 230 fishes, caught in gill nets, about twenty-two miles east of Waukegan in Lake Michigan (August 15), which were inspected on the boat as they were cleaned, although the majority were parasitized by tapeworms.

Ictiobus bubalus (small-mouth buffalo). Of thirty-six fishes examined at a fish market in Havana (August 28), one showed cysts of *Myxobolus ovatus* n. sp. (p. 20) in the integument. Twenty more examined at a Pekin market did not show any infection.

Carpiodes velifer (silver carp). Of the three fishes caught in the Illinois River at Meredosia (September 3), one specimen, 7 cm. long, showed a light infection by *Myxobolus obliquus* n. sp. (p. 25).

Catostomus commersonii (common sucker). Eight large fishes caught in the Fox River near Dundee were free from any recognizable protozoan infection.

C. nigricans (hog sucker). Four fishes caught in the Fox River near Dundee (August 12 and 13) were apparently free from any protozoan infection.

Moxostoma anisurum (white-nosed sucker). Thirty-five fishes were seined in the. Fox River near Dundee (August 12 and 13). Of these, twenty showed large isolated tumors on, or near the base of, the anal or caudal fin (Figs. 7 and 14). The tumors were covered by a reddish network which gave them a characteristic appearance. Microscopical examination revealed that the growths were due to the presence of numerous cysts of *Myxobolus congesticius* n. sp. (p. 26). Both of the two fishes caught in the same river at Carpentersville were infected by another myxosporidian, *Myxobolus gravidus* n. sp. (p. 22), which formed small cysts in the integument and fins.

M. aureolum (common red-horse). Of the ten fishes obtained from the Fox River near Dundee (August 12), one was infected by a myxosporidian, *Myxobolus vastus* n. sp. (p. 21), which was represented by three conspicuous cysts located on three different scales.

M. breviceps (short-headed red-horse). Of the twenty-three fishes caught in the Fox River near Dundee (August 12 and 13), twelve were infected by cysts of a myxosporidian, *Myxobolus conspicuus* Kudo (p. 27), (Figs. 15 and 16). As was noted before (Kudo, 1929), these cysts were confined to the head region of the host fish.

Cyprinus carpio (carp). Two young carp seined in the Fox River near Carpentersville (August 14) and three caught in a creek near Rockford (August 18) were free from any noticeable protozoan parasites. The carp examined at fish markets in Depue, Peoria, Pekin,

Havana, Liverpool, and Quincy, totaling 165 in number, appeared also free from any protozoan infection.

In large reservoirs located in the vicinity of Peoria which were supplied with the water from several springs, there were noted large numbers of carp suffering from an extremely heavy infection by a parasitic ciliate, *Ichthyophthirius multifiliis*. A dozen of them were caught by a net without difficulty, since they were lying in the shallow water along the bank. The integument, the gills (Fig. 8), and the mucous membrane of the buccal cavity, all were so heavily infected by this protozoan that the entire fish appeared whitish in color. In addition, Cyclochaeta, another ciliate, and Costia, a flagellate, were found abundantly, especially in the lesions which Ichthyophthirius produced. As a result of the infection the fishes appeared extremely weakened. It was said that the reservoirs had had an unusual thick growth of vegetation prior to the author's visit, and this obviously had limited the activity of the fish, prevented rapid flow, and brought about a rise in temperature of the water. Undoubtedly these changes were favorable for the growth and reproduction of the ciliate at the expense of the carp, and the epidemic resulted. Ichthyophthirius infection has world-wide distribution, and it is not uncommon to find heavy infection in young fishes kept in small aquaria, but it is certainly remarkable that such an epidemic should occur among fully grown fishes kept in large outdoor ponds.

Campostoma anomalum (dough-belly). Of the eleven fishes seined in a small creek running by the state fish hatchery near Rockford (August 18), one showed in its fins small cysts (Fig. 32) of a myxosporidian, *Henneguya crassicauda* n. sp. (p. 31).

Pimephales notatus (blunt-nosed minnow). Of forty-two fishes seined in the Rock River near Sterling (August 19), two were infected by *Thelohanellus notatus* (Mavor) (p. 29) which formed cysts in the head and body. One fish showed golden cysts (Fig. 9) of *Myxobolus aureatus* Ward (p. 28) in the fins. Several had ectoparasitic copepods attached to the dorsal fin, which resembled, to a certain extent, myxosporidian cysts, but which quickly fell off as the fishes were brought out of the water.

Notropis cornutus (common shiner). Of the eighteen fishes seined in a small creek near Rockford (August 18), one exhibited a large tumor on the left side of the body just behind the head. Microscopical examination revealed that this large growth was due to an infection by a myxosporidian, *Thelohanellus notatus* (Mavor).

Ictalurus furcatus (blue cat). Six fishes, one of which weighed 20 pounds, examined near Brookport (September 9), were apparently free from any histozoic protozoan infections.

I. punctatus (channel cat). Of the twelve fishes caught in the Fox River near Dundee (August 13), two exhibited several cysts of *Henneguya exilis* Kudo in the gills (Fig. 6). Twenty-nine more were examined at a fish market in Havana (August 28), and the gills of two of them showed one and two cysts, respectively, of the same myxosporidian. Three fishes obtained from the Illinois River at Meredosia (August 30) were free from protozoan parasites.

Ameiurus melas (black bullhead). Two fishes collected from the Fox River at Dundee (August 13) were free from any protozoan parasites seen by external examination. The same was true of eight others inspected at a fish market in Havana (August 28).

Esox lucius (northern pike). Two fishes caught in the Fox River near Dundee (August 13) were free from any protozoan infection.

Eucalia inconstans (brook stickleback). Twenty-two specimens collected from a spring-fed pool near Rockford appeared uninfected by any cnidosporidian parasite.

Pomoxis annularis (white crappie). Eighteen specimens observed at Dundee, Rockford, Sterling, and Meredosia were apparently free from protozoan infections.

P. sparoides (black crappie). Twenty caught by fishermen in the Illinois River above Meredosia were free from any histozoic protozoan parasites. One showed growths on the tail fin which resembled closely the lymphocystis cells which had been known to occur in certain marine fishes in European waters, but which have not been recorded from any North American fish.[1]

Ambloplites rupestris (rock bass). Nine fishes collected from the Rock River at Dundee (August 12) did not show any infection by histozoic protozoans.

Lepomis pallidus (bluegill). Forty specimens examined at Dundee, Spring Grove, Rockford, Sterling, and Meredosia were apparently free from any protozoan infections.

Chaenobryttus gulosus (warmouth bass). Six fishes obtained at Meredosia from the Illinois River did not show any histozoic protozoan parasites.

Eupomotis gibbosus (pumpkinseed). Thirty-eight fishes caught in the Fox River near Dundee, in the Rock River near Rockford, and in the Illinois River near Meredosia, showed no noticeable protozoan parasites.

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[1]Since that time several other species of fish were found to possess similar growths. Their study is under way and will be reported elsewhere.

Micropterus dolomieu (small-mouth black bass). One seined in the Fox River at Carpentersville (August 14) and eight kept in a tank at Spring Grove hatchery (August 16) did not show any abnormality which could be attributed to protozoan infection.

M. salmoides (large-mouth black bass). Thirty-four fishes were examined alive in the water at the hatcheries at Spring Grove, Rockford, Wyanet, and Meredosia. None showed any protozoan infection. Some individuals had diffused dark-pigmented areas on the body surface, but there was no indication that the peculiarity was due to parasitic Protozoa.

Perca flavescens (yellow perch). About 100 "dressed" fishes examined at a fish market in Waukegan (August 14) did not exhibit any recognizable protozoan infection. The same was true with three fishes seined in the Fox River near Dundee (August 12 and 13).

Boleosoma nigrum (Johnny darter). Twenty-seven fishes seined in the Fox River near Carpentersville (August 14) appeared free from any visible protozoan infection.

Etheostoma coerulcum (rainbow darter). Twenty fishes seined in the Fox River near Carpentersville did not show any protozoan parasites.

E. flabellare (fan-tailed darter). Twelve fishes caught in the Fox River near Carpentersville were free from abnormalities due to parasitic Protozoa.

Roccus chrysops (white bass). Nine fishes examined at Dundee, Sterling, and Meredosia did not show any protozoan infection.

Aplodinotus grunniens (sheepshead). Some 100 fishes were examined at a fish market in Davenport, Iowa (August 21). They had been caught in the Mississippi River in the vicinity of that city and were dead when examined. None showed any infection by histozoic Protozoa visible to the naked eye. While the fishes were being cleaned, the contents of forty gall bladders were examined microscopically, of which twenty-seven contained a few scattered spores and disporoblastic pansporoblasts of a myxosporidian, *Myxidium aplodinoti* n. sp. (p. 15), which floated in the bile. Trophozoites were completely disintegrated already. As is usually the case with a light myxosporidian infection in this organ, the bladder and the bile did not appear much different from those of a normal fish. The gall bladders of two fishes dissected and examined at a fish market in Shawneetown (September 11) were not infected by the myxosporidian. In the intestine of one fish enormous numbers of a flagellate, *Octomitus* sp., were observed.

The observations are summarized in the accompanying table.

Species of Fish	Fishes Examined	Fishes Infected	Protozoan Parasites
Polyodon spathula.................	15	...	
Lepisosteus osseus................	6	...	
Amia calva......................	6	...	
Dorosoma cepedianum............	56	...	
Argyrosoma artedi...............	330	...	
Ictiobus bubalus.................	56	1	Myxobolus ovatus
Carpiodes velifer................	3	1	M. obliquus
Catostomus commersonii.........	8	...	
C. nigricans.....................	4	...	
Moxostoma anisurum............	37	20	M. congesticius
		2	M. gravidus
M. aureolum....................	10	1	M. vastus
M. breviceps....................	23	12	M. conspicuus
Cyprinus carpio.................	182	12	Ichthyophthirius multifiliis
			Cyclochaeta sp.
			Costia necatrix
Campostoma anomalum..........	11	1	Henneguya crassicauda
Pimephales notatus..............	42	2	Thelohanellus notatus
		1	Myxobolus aureatus
Notropis cornutus...............	18	1	Thelohanellus notatus
Ictalurus furcatus...............	6	...	
I. punctatus....................	44	4	Henneguya exilis
Ameirus melas..................	10	...	
Esox lucius.....................	2	...	
Eucalia inconstans...............	22	...	
Pomoxis annularis...............	18	...	
P. sparoides....................	20	...	
Ambloplites rupestris............	9	...	
Lepomis pallidus................	40	...	
Chaenobryttus gulosus...........	6	...	
Eupomotis gibbosus..............	38	...	
Micropterus dolomieu............	9	...	
M. salmoides...................	34	...	
Perca flavescens.................	103	...	
Boleosoma nigrum...............	27	...	
Etheostoma coeruleum...........	20	...	
E. flabellare....................	12	...	
Roccus chrysops.................	9	...	
Aplodinotus grunniens...........	100	...	
Gall bladder................	42	27	Myxidium aplodinoti
Intestine...................	2	1	Octomitus sp.

Thus the present survey shows that the fishes belonging to three families were more or less frequent hosts to parasitic Protozoa. Of the three species belonging to the family Siluridae (the catfishes), the gills of about 9 per cent of *Ictalurus punctatus* examined were infected by a myxosporidian, *Henneguya exilis*. On the other hand, each of the four species belonging to the family Cyprinidae (the minnows and carp) was host to a protozoan parasite. The observation made in the vicinity of Peoria indicates that a heavy Ichthyophthirius infection in adult fishes kept in a large outdoor reservoir may follow certain changes in the physical conditions of the water. A myxosporidian parasite was observed in each

of the other three species of fish in either the fins or integument. About 2 per cent of *Pimephales notatus* were parasitized by *Myxobolus aureatus,* and *Thelohanellus notatus* was observed in about 5 per cent of both *Pimephales notatus* and *Notropis cornutus* examined, while *Henneguya crassicauda* was found in one out of 11 *Campostoma anomalum.*

The myxosporidian infection was, however, quite common in five out of seven species studied belonging to the family Catostomidae (the suckers). Each of four species harbored a myxosporidian, while the fifth was host to two species of Myxosporidia. The occurrence of *Myxobolus congesticius* in 20 out of 37 *Moxostoma anisurum* and of *Myxobolus conspicuus* in 12 out of 23 *Moxostoma breviceps* would indicate that these two myxosporidians were very common parasites in these fishes in the Fox River at the time of examination. Aside from *Myxobolus obliquus* which was observed in the body muscle fiber of *Carpiodes velifer,* the five species of Myxosporidia attacked either fins or integument of the host body.

Since the myxosporidian infections were in no case severe and were confined in almost all the fishes to the extremities or superficial portions of the body, it did not appear that they brought about any harmful effects. It must, however, be remembered that lesions produced by them become often the foci of secondary fungous or bacterial infections which may result in the death of the host. The solution of various problems brought out through the present survey awaits more intensive studies.

DESCRIPTIONS OF THE SPECIES OF MYXOSPORIDIA FOUND PARASITIC IN FISHES OF ILLINOIS

In the following pages are given descriptions of several new species and additional information on a few already known species of Myxosporidia which were found parasitic in some of the fishes inhabiting the waters of Illinois. As to the former records of the Myxosporidia reported from Illinois, the reader is referred to Kudo (1920, 1920a, and 1929).

Each species described below was compared carefully as far as possible with the known species of the genus (Kudo, 1933) to which it belongs with respect to the characters of both the spore form and the vegetative form. The spores of one species were studied in life. Those of all other species were examined in material preserved in formol (4 per cent), which would give somewhat smaller dimensions than fresh spores (Kudo, 1921). To facilitate future comparison, dimensions of preserved, unstained spores as viewed in water suspension, are given.

Myxidium aplodinoti n. sp.
(Figs. 35-38)

HABITAT.—In the gall bladder of the sheepshead, *Aplodinotus grun-niens*. From the Mississippi River in the vicinity of Davenport, Iowa (August 21, 1930). The host organ of twenty-seven out of forty fishes brought into a market exhibited a light infection by this myxosporidian.

VEGETATIVE FORM.—The host fish had been dead for some time when examined, and the vegetative forms had apparently disintegrated. Isolated spores and a few disporoblastic pansporoblasts were noted. This myxosporidian is probably polysporous.

SPORE.—Fusiform. The shell-valves are slightly asymmetrical; each with seven to nine striae which run parallel to the sutural line. Extremities are either bluntly or sharply pointed. Sutural line distinct though delicate. The polar capsules are broadly pyriform or subspherical. The sporoplasm is finely granulated and contains two nuclei. Dimensions of fresh spores: length 11-12 μ, width and thickness 5-6 μ, polar capsules 4-5 μ by 3-3.5 μ.

Myxosoma grandis n. sp.
(Figs. 1, 2, 17, and 39-42)

HABITAT.—In the liver of the silver-mouthed minnow, *Ericymba buccata*. The five infected fishes, measuring from 5 to 10 cm. long, were collected from the Salt Fork, a tributary of the Vermilion River, in the vicinity of Rantoul and Thomasboro (July and August, 1928, and November, 1929). All were preserved in formol when examined.

VEGETATIVE FORM.—As far as can be determined the myxosporidian was present in the liver only, other organs such as the heart, kidneys, intestine, etc., being free from the parasite. These fishes, unlike healthy ones, showed a great distension of the body below the pectoral fins (Fig. 1), a condition which was found to be due to an enormously enlarged liver. This organ not only pushed aside other organs of the body cavity, but forced the abdominal wall to distend to such an extent that a characteristic deformity resulted; in one fish the abdominal wall was ruptured along the median ventral line, no doubt because of the extreme enlargement of the liver which measured 10 by 10 mm. None of the infected fish was observed alive, but it is not difficult to see the fatal outcome of such an infection upon the host fish.

Viewed in section preparations, the host organ was heavily loaded with an enormous number of vegetative forms, varying in diameter from 50 to 250 μ. The majority contained highly reticulated cytoplasm, in which were located mature spores, and were somewhat angular in outline

due to the mechanical pressure received from adjacent parasites. Each vegetative form was completely surrounded by what seemed to be highly flattened cells of the host's tissue. Younger individuals contained less reticulated cytoplasm and were grouped here and there among the more numerous mature forms. They were compactly filled with characteristic nuclei and developing pansporoblasts and measured from 30 to 100 μ in the largest diameter. The pansporoblast is typically disporoblastic. Polysporous.

SPORE.—Ellipsoidal with bluntly drawn-out anterior, and broadly rounded posterior end in front view; pyriform in side view; lenticular in end view. The shell-valves are symmetrical, and the sutural ridge is broad. Five to ten triangular markings are observable along the posterior half of the shell in the majority of spores. The two polar capsules are elongated, pyriform, and convergent. The sporoplasm is comparatively large, uniformly granulated, and does not contain any iodinophilous vacuole. When stained, two vesicular nuclei become distinctly visible. Dimensions of spores: length 15-16 μ, breadth 9-11 μ, thickness 6-8 μ, polar capsules 6-7 μ by 2.5-3 μ.

Myxosoma procerum n. sp.
(Figs. 3, 18, and 43-46)

HABITAT.—In the integument of the trout-perch, *Percopsis guttatus*. From the Illinois River at Meredosia, June 10, 1928, and Quiver Lake, Havana, January, 1931. A single fish 6 cm. long from Meredosia showed numerous small rounded cysts in the integument and the caudal fin. These cysts were scattered over the entire body surface but were more abundant on both sides of the posterior region. The cysts appeared whitish in formol and measured about 0.5 to 1.5 mm. in diameter. Section preparations showed that the cysts were located in the connective tissue directly below the scales. One or two to several cysts were found under a single scale.

Six fishes from the latter locality, on the other hand, showed smaller numbers of cysts which, however, were much larger and more conspicuous and were distributed on the sides of the body or at the base of fins, a few being noted in the head. The fishes which measured from 6.5 to 7 cm. in length, harbored 4, 4, 5, 7, 10, and 24 cysts, respectively. These cysts, like those described above, were whitish in formol and were easily recognized with the naked eye. In surface view they were irregularly rounded to spherical in outline, 1 to 2.5 mm. in their longest diameters; but hemispherical in side view, extending 0.5 to 1 mm. above the level of the body surface. The seat of infection was similar to that which was found in the fish from the first locality.

VEGETATIVE FORM.—Viewed from the surface, the cysts are more or less circular, but somewhat flattened as noted in cross-section of the host's integument, measuring 155 by 80 μ up to 960 by 260 μ. Each cyst is surrounded by a relatively thick envelope composed of the connective tissue of the host. There is a zone, about 10 μ thick, of finely granulated cytoplasm in the peripheral part. Toward the center enormous numbers of nuclei, generative cells, disporoblastic pansporoblasts, and spores occur in the reticulated cytoplasm. Polysporous.

SPORE.—Elongated ellipsoid in front view; lenticular in side view. Shell is relatively thin; shell-valves are symmetrical. The sutural ridge is broad, but sutural line indistinct. Two polar capsules are equally large and elongate pyriform. The sporoplasm is either granulated or somewhat vacuolated, but does not possess any iodinophile vacuole. When stained, two vesicular nuclei become visible; they do not show any endosome. Dimensions of spores: length 15-17 μ, breadth 6.5-7 μ, thickness 5-6 μ, polar capsules 7-9 μ by 1.5-2 μ.

Myxosoma robustum n. sp.
(Figs. 4, 19, and 47-50)

HABITAT.—In the connective tissue of the integument of the common shiner, *Notropis cornutus*. Rock River near Newbury (August 20, 1926). A single formol specimen, 5.5 cm. long, showed a large tumor on the left side of the body behind the operculum. It was irregularly rounded, measuring 1.3 cm. in the largest diameter, protruding about 3 mm. above the general level of the body surface and projecting some 4 mm. into the body cavity.

VEGETATIVE FORM.—The tumor was due to the presence of an enormous number of comparatively small trophozoites situated in the connective tissue between the epidermis and the body musculature. These trophozoites are spherical or oval in shape and measure from 20 to 50 μ (exceptionally up to 150 μ) in diameter. There are extremely large numbers of blood vessels of various dimensions penetrating through the entire group of the parasites. It is presumed that in life the tumor was quite reddish in color, judging from these blood vessels present within it. Each trophozoite was densely filled with numerous nuclei, generative cells, disporoblastic pansporoblasts, and spores. Polysporous.

SPORE.—Ellipsoidal in front view; fusiform in side view. The shell is comparatively thick and shows in the front view five to eight folds along the posterior margin. Two polar capsules are elongated pyriform and convergent. The sporoplasm occupies about one-half of the intrasporal space. It contains no iodinophile vacuole, but when stained shows

two nuclei, each with a centrally located endosome. Dimensions of spores: length 14-16 μ, breadth 10-11 μ, thickness 7-8 μ, polar capsules 6.5-7.5 μ by 2.5 μ.

Myxosoma bibullatum n. sp.
(Figs. 21 and 51-54)

HABITAT.—In the integument of the sucker, *Catostomus commersonii*, collected from the Rock River near Beloit (May 3, 1927). The fish, 5.5 cm. long, showed a hemispherical tumor on the ventral side close to the left pectoral fin. It measured 1.25 mm. in diameter.

VEGETATIVE FORM.—The tumor contained a single cyst situated in the subepithelial connective tissue. It was nearly spherical and was filled with developing and mature spores. The pansporoblast is disporoblastic. Polysporous.   •

SPORE.-- Oval in front view; lenticular with somewhat drawn-out ends in side and end views. The shell is relatively thick, and both the sutural ridge and line are distinct. Two or rarely three radiating thickenings on the shell give a characteristic appearance to the spore. These thickenings are seemingly due to prolonged existence of the two unusually large valve cell nuclei (Figs. 21 and 53). Two polar capsules are broadly pyriform with often a long drawn-out duct. The sporoplasm is large and possesses no iodinophile vacuole. When stained, it shows two vesicular nuclei, each containing an endosome and numerous peripheral chromatin granules. Dimensions of spores: length 14-15 μ, breadth 11.5-12.5 μ, thickness 6-7.5 μ, polar capsules 7 by 3.5 μ.

Myxobolus squamosus n. sp.
(Figs. 5 and 55-63)

HABITAT.—In the connective tissue below the scales of the river chub, *Hybopsis kentuckiensis*. From the Sangamon River near Dewey (August 12, 1928). Two infected fishes were preserved in formol.

VEGETATIVE FORM.—This myxosporidian produces conspicuous cysts in the corium, directly below the scales. These cysts are distinctly contoured, vary in form from circular to rectangular, and are confined within the outer half of the infected scales. When an infected scale was taken from the host fish, the entire cyst was also removed. One fish, 8.6 cm. long, harbored 22 and 18 cysts on the left and right sides, respectively, while the other fish, 9 cm. long, showed 2 and 9 cysts on the corresponding sides. The cysts were distributed over the entire body with the exception of the head and fins. Preserved in formol, they were milky white and varied from 0.8 to 2 mm. in the largest diameter. In section preparations it was noted that the cysts were greatly flattened. The highly re-

ticulated cytoplasm contained numerous nuclei, developing pansporoblasts which were disporoblastic, and mature spores. Polysporous.

SPORE.—Circular or subcircular in front view; lenticular in side or end view. Two pyriform polar capsules are convergent at the anterior end where there occurs a small intercapsular projection. ·The sporoplasm occupies the posterior portion of the spore and shows a large conspicuous iodinophile vacuole. The shell-valves are relatively thick and exhibit two to seven or eight triangular markings in front view. When stained, two comparatively small nuclei without endosome are noticeable in the sporoplasm. Dimensions of spores: length and width 8-9 μ, thickness 4.5-5.5 μ, polar capsules 3-4 μ by 1.5-2 μ.

REMARKS.—Of the seventy species of Myxobolus (Kudo, 1933) two species—*M. transovalis* Gurley 1893 and *M. squamae* Keysselitz 1908—occur under the scales of fresh-water fish. These two species differ from the species under description in the major characters of the spore. The spores of *M. mülleri* Bütcshli and *M. exiguus* Thélohan (Kudo, 1920) resemble those of the present species. But the vegetative form of the species under consideration is entirely different from that of either of the two species mentioned above.

Myxobolus teres n. sp.
(Figs. 64-67)

HABITAT.—In the body muscle of the silver fin, *Notropis whipplii*. From the Rock River near Milan (September 22, 1927). The fish, 3 cm. long and preserved in formol, showed an elongated ellipsoidal tumor on the left side of the body directly above the anal fin. The whitish tumor measured 3 mm. by 1.5 mm. and was located parallel to the lateral line. No other cysts were recognized.

VEGETATIVE FORM.—Sections cut at right angles to the body surface showed that the tumor was caused by a single cyst situated in the muscular tissue. It measured 1.75 mm. long and about 0.7 mm. deep. It was in direct contact with the muscle fibers, which showed no noticeable histological changes. Nuclei and disporoblastic pansporoblasts were located, as usual, close to the surface of the cyst, while young and mature spores were scattered throughout the reticulated cytoplasm. Polysporous.

SPORE.—Subspherical in front view; lenticular in side and end views. The shell is uniformly thick and as a rule smooth, although occasionally four or five oblong thickenings are present along the posterior margin. The sutural ridge is conspicuous, but the sutural line is indistinct. Two polar capsules are large, pyriform, and convergent. The sporoplasm is relatively small, but contains a very large iodinophile vacuole. In stained

spores the two nuclei of the sporoplasm are very distinct. Dimensions of spores: length 9.5-11.5 μ, breadth 9-10.5 μ, thickness 5-6 μ, polar capsules 6 by 3 μ.

Myxobolus ovatus n. sp.
(Figs. 68-71)

HABITAT.—In the integument of the small-mouth buffalo, *Ictiobus bubalis*. A fish, 6 cm. long, obtained from the Rock River near Rockford (September 22, 1928), and another, 18 cm. long, examined at a fish market in Havana (August 28, 1930), were infected by the present myxosporidian.

VEGETATIVE FORM.—The smaller fish had an indistinctly outlined and compressed cyst, measuring 1.5 by 1 mm., which was situated about one centimeter back of the posterior end of the gill-cover on the left lateral line. The larger fish had a somewhat more distinct cyst, measuring 2 by 1 mm., near the right ventral fin. In both fishes the cyst was surrounded by the connective tissue of the corium and contained mainly mature spores and a small number of developing disporoblastic pansporoblasts. Polysporous.

SPORE.—Oval with somewhat bluntly pointed anterior end in front view; lenticular in side view. The shell-valves are comparatively thin, and in many spores there are two or three thickenings on the posterior margin. The two polar capsules are equal or only slightly different in size, and the inner walls are arranged parallel to each other. The sporoplasm, which does not fill the remaining part of the intrasporal cavity, contains a conspicuous iodinophile vacuole. When stained, two nuclei, each with a small endosome, become clearly visible. Dimensions of spores: length 11.5-13 μ, breadth 9-10 μ, thickness 7 μ, polar capsules 5.5-6.5 μ by 2.5-3 μ.

Myxobolus angustus n. sp.
(Figs. 10, 20, and 72-75)

HABITAT.—In the gills of the bullhead minnow, *Cliola vigilax*, collected from the Illinois River at Meredosia Bay (June 18, 1928). Three specimens, 2.2 to 2.8 cm. in length and preserved in formol, had several clustered cysts on the gills which could be plainly seen through the operculum.

VEGETATIVE FORM.—The cysts were located in the gill filaments, which were much enlarged. Surrounded by flattened epithelial cells, these cysts were ellipsoidal in general form and varied in size from 150 by 6 μ to 260 by 100 μ. All cysts were at advanced stages of development, and

filled with mature spores and developing disporoblastic pansporoblasts. Polysporous.

SPORE.—Pyriform. The sutural ridge is distinct, but the sutural line indistinct. The shell is relatively thin, and shows a somewhat rough surface at the posterior margin, which stains deeply. Two polar capsules are elongated pyriform and equal or nearly equal in size. The sporoplasm is comparatively small and has a large iodinophile vacuole. When stained, the two nuclei are most often found in a point close to the posterior ends of the capsules. Dimensions of spores: length 14-15 μ, breadth 7-8 μ, thickness 6-7 μ, polar capsules 8-9.5 μ by 2.5-3 μ.

Myxobolus vastus n. sp.
(Figs. 76-81)

HABITAT.—In the corium above the scales of the common redhorse, *Moxostoma aureolum*. From the Fox River near Dundee (August 12, 1930). A large fish, 31 cm. long, showed three whitish tumors on the left side of the body. These tumors were ellipsoidal or circular in form, measured 3 by 1.5 by 1 mm., 4.2 by 2 by 2 mm., and 1 mm. in diameter by 0.5 mm. high, and were situated in the integument above the scales. Microscopical examination revealed that each tumor was composed of a single cyst surrounded by a thick envelope of the host tissue.

VEGETATIVE FORM.—In section preparations of the first two tumors, it was noted that the epidermis above the parasites was much thinned at places, while the connective tissue around them was greatly hypertrophied and was penetrated by a large number of anastomosing blood vessels and capillaries. The cysts were smoothly and distinctly outlined and measured 2.5 mm. and 3.8 mm., respectively, in the largest diameter. The homogeneous peripheral zone of cytoplasm was narrow, and the pansporoblasts, which were disporoblastic, were comparatively small in number, while an enormous number of spores occupied the greater central portion. Polysporous.

SPORE.—Oblong in front view; narrowly lenticular in side view. The shell is moderately thick and exhibits in many spores some seven radiating lines on the posterior margin. The sutural ridge is somewhat thickened at the ends, but the line is indistinct. Two polar capsules are pyriform, and the capsulogenous nuclei seem to remain for some time after the spore has matured. The sporoplasm is granulated and contains a large iodinophile vacuole. When stained, it shows two comparatively small nuclei. Dimensions of spores: length 9.5-10.5 μ, width 7.5-8 μ, thickness 4-4.5 μ, polar capsules 4.5-5.5 μ by 1.5-2.5 μ.

Myxobolus gravidus n. sp.

(Figs. 82-84)

HABITAT.—In the integument and fins of the white-nosed sucker, *Moxostoma anisurum*. From the Fox River near Carpentersville (August 14, 1930). One specimen, 11 cm. long, showed three cysts: two on the base of the tail fin and one on the left pectoral fin. The second fish, 12 cm. long, exhibited six cysts: three on the sides of the head and three on the ventral side of the body between the pectoral fins. All cysts were rounded and measured less than 0.5 mm. in diameter.

VEGETATIVE FORM.—The myxosporidian was studied in smears only, and therefore the exact seat of infection and the cytological detail of the cysts are unknown. However, it was observed that the pansporoblasts were disporoblastic. Polysporous.

SPORE.—Oval to oblong in front view; broadly fusiform in side or end view. The shell is moderately thick, with four to six folds on the posterior part. The sutural ridge is inconspicuous. Two polar capsules are pyriform and convergent. The sporoplasm is relatively large and contains an iodinophile vacuole and ordinarily two nuclei with a large endosome. Dimensions of spores: length $12\text{-}14\,\mu$, width $9.5\text{-}10\,\mu$, thickness $7\,\mu$, polar capsules $5\text{-}5.5\,\mu$ by $2.5\,\mu$.

Myxobolus compressus n. sp.

(Figs. 13 and 85-88)

HABITAT.—In the connective tissue of the integument of the straw-colored minnow, *Notropis blennius*. From the Rock River near Beloit (May 3, 1927). Six infected fishes, 4 to 4.5 cm. long, were preserved in formol. One fish was also infected by *Thelohanellus notatus*. To the unaided eye the body surface appeared uneven and the scales were somewhat lifted, so that the host fish presented a very characteristic appearance (Fig. 13). Unlike other Myxobolus cysts, individual cysts were indistinctly outlined.

VEGETATIVE FORM.—Examination of the sections of the integument revealed that enormous numbers of trophozoites were located in the connective tissue of the corium above and below the scales, which condition is without doubt responsible for the peculiar external appearance of the diseased fish. These vegetative forms were circular to irregularly rounded in surface view and extremely flattened, so that two or three or even five such trophozoites were situated one above the other between the scale and the epidermis. The host cells which were in direct contact with the myxosporidian body became much distended and the protoplasmic contents were apparently absorbed by the parasite, while the cell wall persisted, which resulted in the radiating cytoplasm along the periphery in

the trophozoite of the present myxosporidian. These cysts varied in size and measured from 300 to 600 μ in the largest diameter and about 50 to 100 μ thick, tapering gradually toward the periphery. They appeared somewhat like the trophozoites of coelozoic Myxosporidia such as *Zschokkella acheilognathi* (Kudo, 1920), and were very different from the Myxobolus cysts ordinarily met with. In the reticulated cytoplasm of the cyst were found numerous nuclei, developing disporoblastic pansporoblasts, and spores. Polysporous.

SPORE.—Ovoid to broadly ellipsoid in front view; broadly spindleform in side view. The shell is uniformly thick, and exhibits about six small triangular markings along the posterior margin. The sutural ridge is moderately wide, with a distinct sutural line. One of the peculiar characteristics of this myxosporidian is the persistence of the capsulogenous cells and their nuclei, both of which remain visible long after the maturing of the sporoplasm. The granulated sporoplasm is relatively large and contains a large iodinophile vacuole and two nuclei filled with fine chromatin granules. Dimensions of spores: length 12-14 μ, width 7-10 μ, thickness 7-7.5 μ, polar capsules about 5 by 2.5 μ.

Myxobolus mutabilis n. sp.
(Figs. 11, 12, and 89-93)

HABITAT.—In the integument of the head and fins of the blunt-nosed minnow, *Pimephales notatus*. From the Rock River near Beloit (May 2 and 3, 1927). Seventeen fishes were preserved in formol. The distribution of the cysts upon the bodies of the hosts is shown in the accom-

Fish		Number of the Cysts	
Number	Length (cm.)	In Head	In Other Parts
1.....................	3.8	32	
2.....................	3.6	24	3 on base of the left pectoral fin
3.....................	4.3	4	1 near the left pectoral fin
4.....................	4.5	36	25 on ventral and pectoral fins
5.....................	3.8	8	2 on the right pectoral fin
6.....................	4.0	22	1 on the left pectoral fin
7.....................	4.0	17	3 near the right pectoral fin
8.....................	6.3	30	12 on pectoral fins
9.....................	6.0	19	9 on pectoral fins
10....................	5.0	23	
11....................	4.5	33	
12....................	4.0	10	
13....................	4.2	6	
14....................	4.6	16	
15....................	4.7	8	
16....................	4.2	9	
17....................	5.0	12	

panying tabulation. The head region was most frequently infected. Infection of the eye was noticed only in one fish (No. 13). The pectoral fins were also often the seat of infection. The cysts were small, measuring less than 1 mm. in diameter. To the naked eye they appeared as small white spots. They were circular or oval in outline, but when grouped they presented very irregular contours.

VEGETATIVE FORM.—The cysts occurred in the connective tissue of the corium. In sections cut at right angles to the host's body surface, they were ellipsoidal in form, with their long axis lying parallel to the body surface, and varied somewhat in size, measuring from 450 by 150 μ to 880 by 250 μ. The peripheral zone of the cytoplasm, about 5 μ in thickness, was finely reticulated, while the remaining part was vacuolated. As is usually the case, numerous nuclei, generative cells, and disporoblastic pansporoblasts were confined to the peripheral portion, while mature spores occupied the central area of the cyst. Polysporous.

SPORE.—Greatly variable in form and size. Typically ellipsoidal with somewhat narrowed anterior half in front view; lenticular in side view. Some spores are, however, nearly spherical. A great variation of form was recognized among spores occurring in one and the same cyst. The shell is relatively thin and smooth. Along the suture of the shell-valves occurs a ribbon-like band encircling the spore. The edge of each valve is thickened so that there appear in profile three ridges on the spore. A similar structure had been noted by Balbiani in *Myxobolus ellipsoides* (Kudo, 1920). The two polar capsules are elongate pyriform and comparatively large. The large sporoplasm contains an iodinophile vacuole and two rather large nuclei. Dimensions of spores: length 9.5-12 μ, breadth 7.5-9 μ, thickness 6-7 μ, polar capsules 5-6.5μ by 2-3.5 μ.

Myxobolus nodosus n. sp.
(Figs. 94-96)

HABITAT.—In the integument of the blunt-nosed minnow, *Pimephales notatus*. From the Rock River near Byron (August 22 and 23, 1927). Twelve fishes, preserved in formol, measured from 2 to 3.5 cm. in length. The myxosporidian produces small isolated cysts, which were especially abundant on the ventral side of the posterior half of body. They were smoothly rounded in outline and measured from 0.5 to 1 mm. in diameter.

VEGETATIVE FORM.—The nearly spherical cysts were lodged in the connective tissue of the corium. The host tissue around the cysts was moderately thickened and the epithelial tissue above the parasites somewhat thinned. Within the cyst there was noted, as is usually the case, a

thin homogeneous peripheral zone of cytoplasm containing numerous nuclei, generative cells, disporoblastic pansporoblasts at various stages of development, and mature spores. Polysporous.

SPORE.—Circular to subcircular in front view; broadly fusiform in side or end view. The shell is uniformly thin, except the posterior one-fourth which shows numerous rounded thickenings, presenting an undulating outline. The sutural ridge is broad and prominent, but sutural line indistinct. Two polar capsules are equal in size and relatively large and broadly pyriform. The sporoplasm is consequently small and contains an iodinophile vacuole. Dimensions of spores: length 9-10.5 μ, breadth 8.5-9.5 μ, thickness 7 μ, polar capsules 5-6 μ by 2.5-3.5 μ.

Myxobolus obliquus n. sp.
(Figs. 23, 24, and 97-101)

HABITAT.—In the body muscle fibers of the silver carp, *Carpiodes velifer*. From the Rock River below Beloit (August 20, 1926; May 20, 1927) and the Illinois River at Meredosia (September 3, 1930). Two fishes from the first locality, 3.5 and 4 cm. long, were preserved in formol. Both specimens showed numerous obliquely directed white bodies embedded somewhat deeply on the sides of the body. Viewed with the naked eye, the smaller fish showed 29 and 18 such bodies on the right and left sides of body, respectively; while the larger fish showed 24 cysts, of which 9 were on the right and 15 on the left side of body. One of three fishes caught in the second locality, 5.5 cm. long, exhibited 5 and 9 cysts on the right and left sides, respectively.

VEGETATIVE FORM.—The cysts are situated in the host's muscle fibers. They are fusiform in general shape and circular in cross-section, measuring 500 μ to 1.8 mm. in length by 60 to 250 μ in diameter. The infected muscle fiber does not show any cytological changes other than an enormous increase in size as the parasite grows. The adjacent fibers appear to be perfectly normal. The cyst is distinctly and smoothly outlined and in direct contact with the host's cell body. The peripheral cytoplasm is granular and contains nuclei, generative cells, and developing pansporoblasts which are disporoblastic. Sporulation was advanced very far in all cysts examined, so that the interior of the cysts was vacuolated and occupied by numerous spores. Polysporous.

SPORE.—Circular or subcircular in front view; lenticular in side or end view. The shell is moderately thick, with five to ten radiating thickenings on it. The sutural ridge is narrow, but the line distinct. Two equal polar capsules are relatively large and convergent. In some spores there

is a small intercapsular projection. The sporoplasm occupies about one-half the cavity of the spore. The iodinophile vacuole is conspicuous. Each of the two nuclei of the sporoplasm contains an eccentric endosome. Dimensions of spores: length 8-9 μ, breadth 7-8 μ, thickness 5-6 μ, polar capsules 4.5 by 2 μ.

Myxobolus bellus n. sp.
(Figs. 22 and 102-105)

HABITAT.—In the integument of the common river carp, *Carpiodes carpio*. From the Kaskaskia River near Carlyle (August 24, 1929). A small portion of the integument taken from one side of the body was preserved in formol.

VEGETATIVE FORM.—A single cyst, 1.8 by 1.2 mm., was lodged in the connective tissue of the integument. The pansporoblast is disporoblastic. Polysporous.

SPORE.—Ellipsoidal or elongate oval in front view; asymmetrically lenticular in side view. The shell is relatively thick and shows regularly three spinous markings near the posterior end. The shell-valves are somewhat asymmetrical. Two polar capsules are comparatively small. The finely granulated sporoplasm contains an iodophile vacuole. When stained, the capsulogenous nuclei are recognizable long after the spore has matured. The sporoplasm is binucleated. Dimensions of spores: length 10-11 μ, breadth 6.5-7 μ, thickness 4-5 μ, polar capsules 4-5 μ by 1.5-2 μ.

Myxobolus congesticius n. sp.
(Figs. 7, 14, 25, and 106-110)

HABITAT.—On the fins of the white-nosed sucker, *Moxostoma anisurum*. From the Fox River near Dundee (August 12, 1930). Of the thirty-five fishes, varying in length from 20 to 30 cm., twenty were infected by this myxosporidian which produced large conspicuous tumors on, or near the base of, the tail or anal fin of the host fish. These tumors measured 3 to 12 mm. long, 1 to 10 mm. wide and 1 to 6 mm. high, and were creamy white in life covered by a red network, which presented a quite typical appearance. On account of the highly distended condition of the tumors, the host's epidermis above the tumors was exceedingly thin and broke easily upon application of a slight pressure, setting free the creamy contents, which were almost exclusively made up of spores.

VEGETATIVE FORM.—The tumors were located in the subepidermal connective tissue, and each was made up of a large number of cysts. The

latter varied in form from spherical to irregularly angular—which seemed to be caused by fusion of two or more cysts and further by the pressure received from adjacent individuals—and measured 300 μ to 1 mm. in the largest diameter. These cysts were so closely associated with one another that only narrow spaces remained between them, and in these spaces were located blood vessels of various dimensions and tissue cells of the host. This condition accounts for the characteristic network on the tumor visible to the unaided eye. Variable in size and form, all cysts showed a similar structure. The outer surface of the cyst was sharply delimited from the host's tissue. Along the periphery there was a uniformly thick (8 to 15 μ) homogeneous cytoplasmic zone in which no special structures were noticeable. Towards the central portion the cytoplasm was much vacuolated and contained numerous nuclei, generative cells, and disporoblastic pansporoblasts. Polysporous.

SPORE.—Circular or oval in front view; lenticular in side or end view. The shell is moderately thick and in many cases possesses fine radiating folds or markings which are visible in front view. The sutural ridge is wide and conspicuous, but the line indistinct. Two polar capsules are pyriform and convergent. In the sporoplasm is located a relatively large iodinophile vacuole. The sporoplasmic nuclei are often observed in unstained condition. They are frequently closely associated with each other in the direction at right angles to the sutural plane. Abnormal spores occur in this species as in others. One spore for example showed a single polar capsule in its normal position, while the other polar capsule appeared to be lodged in the shell, which may be due to an early development of the polar capsules in the present species. Dimensions of spores: length 9-10 μ, breadth 8.5-9.5 μ, thickness 6 μ, polar capsules 5-6 μ by 2.5-3.5 μ.

Myxobolus conspicuus Kudo
(Figs. 15 and 16)

This myxosporidian was first observed in the short-headed redhorse, *Moxostoma breviceps*, collected from the Rock River at Rockford in November and December, 1925 (Kudo, 1929). It was found further in twelve out of twenty-three fishes of the same species seined in the Fox River near Dundee (August 12 and 13, 1930). It produces conspicuous cysts in the integument of the head of the host. Vegetative forms and spores have already been described (Kudo, 1929), and no additional information except its occurrence was obtained by the study of recent material.

Myxobolus aureatus Ward
(Figs. 9, 26-28, and 111-115)

HABITAT.—In the fins of the blunt-nosed minnow, *Pimephales nota-tus*. This myxosporidian was first observed in a specimen, 2.5 cm. long, caught in Lake Decatur (July 30, 1929). One of the fishes collected from the Rock River near Sterling (August 19, 1930) was also infected by it. Of many fishes, collected from the Fox River in the vicinities of Carpentersville, St. Charles, and Johnsburg (July 30 to August 20, 1930), eighty-four specimens, 1.9 to 3.8 cm. long, were heavily infected by the same protozoan. All fins were subject to infection, but pectoral and ventral fins were in most cases most frequently and heavily attacked. Of these paired fins there was no noticeable difference in intensity of infection between the two sides. The number of cysts occurring on various fins of individual fishes varied from 2 to 63, although in the majority of the fishes 4 to 15 cysts were commonly encountered. The one fish caught at Sterling showed yellow-colored cysts as was noted by Ward (Kudo, 1920). All other fishes were preserved in formol. The cysts were opaque, white, and very conspicuously visible to the naked eye because of their location on the fins. One of the characteristics of these cysts is the presence of numerous enlarged chromatophores scattered through the host tissue surrounding them. The larger cysts were oblong, ovoid, or ellipsoid and measured from 0.5 to 1 mm. in the largest diameter, while the smaller cysts were as a rule nearly spherical and measured from 0.1 to 0.3 mm. in diameter, being almost invisible to the unaided eye.

VEGETATIVE FORM.—The cysts are spherical or ellipsoidal in cross-section. When several cysts occur together, they assume various forms due to the mutual pressure. The largest diameter of the cysts varied in cross-section from 100 to 1000 μ. The cysts are located in the connective tissue of the fins, in which a far greater number of blood capillaries occur than in healthy tissue. This is probably responsible for the striking abundance and hypertrophy of chromatophores around the cysts. Except for a narrow peripheral zone, all of the cysts were vacuolated and filled with developing and mature spores. The pansporoblast is disporoblastic. Polysporous.

SPORE.—Pyriform with bluntly pointed anterior and broadly rounded posterior ends. The sutural ridge is narrow but distinct; the line also is distinct. The posterior portion of each shell-valve is slightly constricted near the sutural ridge. In some spores there are seen two narrow ridges running from the latero-posterior margin to a point near the center of the spore. Two polar capsules, which are equal or slightly different in size, are comparatively long and show plainly their coiled filaments. The sporoplasm is finely granulated and contains an iodinophile vacuole and

two nuclei which are often recognizable in unstained conditions. Dimensions of spores: length 12-14.5 μ, breadth 7-8 μ, thickness about 7 μ, polar capsules 8-10 μ by 2.5-3 μ.

REMARKS.—There are slight differences in size of spores and cysts, and in the host species, between the form described above and *Myxobolus aureatus* Ward from Lake Erie. They are, however, too small to consider the present form as a new species.

Thelohanellus notatus (Mavor)

(Figs. 116-118)

The genus Myxobolus comprises, as set forth by Thélohan in his classification, the Myxosporidia with tailless spores, each containing an iodinophile vacuole and one or two polar capsules. In a recent paper (Kudo, 1933) it was proposed to separate the unicapsulated species from the bicapsulated forms, and there was established a new genus, Thelohanellus, to which all unicapsulated Myxobolus were transferred, and Myxobolus was retained for bicapsulated species. Accordingly *Myxobolus notatus* Mavor is now designated as *Thelohanellus notatus* (Mavor).

HABITAT.—This myxosporidian was hitherto observed in the blunt-nosed minnow, *Pimephales notatus*, from the waters of North America (Kudo, 1929). Examination of material on hand shows that it occurs also in several other species of fishes in Illinois. Two specimens of this minnow caught in the Rock River near Sterling (August 19, 1930) harbored the protozoan. One fish had a white cyst, 2 mm. in diameter, on the ventral side of the head. The cyst was situated within the connective tissue of the integument. The other fish had two cysts, both about 1.5 mm. in diameter, near the dorsal fin on the right side of the body. They were also located in the subepidermal connective tissue.

The bullhead minnow, *Cliola vigilax*. From the Rock River (June, 1925). In a single fish preserved in formol, a tumor was noted on the anterior left side of the body. It was oblong in outline and measured 5 mm. in the largest diameter. This tumor was due to the presence of a large cyst located in the hypertrophied subepidermal connective tissue.

The common shiner, *Notropis cornutus*. Near Rockford (August 18, 1930). In one fish a large tumor, 7 mm. in the longest diameter and raised 3 mm. above the general body surface, was recognized just behind the head on the left side. In sections, an almost spherical cyst was found within the tumor, which was surrounded by a thick layer of subepidermal connective tissue of the host fish, containing a large number of blood vessels and capillaries.

The straw-colored minnow, *Notropis blennius*. Rock River near Beloit (May 3, 1927). Of three fishes, preserved in formol, one had two cysts: one on the dorsal side just in front of the dorsal fin and the other on the right side near the anal fin. The second fish showed one cyst situated on the base of the right pectoral fin. The third fish exhibited two cysts: one on the left side near the tail fin and the other below the dorsal fin on the right side of the body. The seat of infection was the same as that mentioned above.

VEGETATIVE FORM.—The cysts were surrounded by the connective tissue of the integument of the host fish. The host tissue which was in direct contact with the parasite underwent a peculiar change as noted before (Kudo, 1929). The cytological observation of the cysts did not yield any new data.

SPORE.—The spores taken from cysts occurring in the four different host species are indistinguishable from one another. Elongated pyriform, but often broadly pyriform which are obviously not fully mature. A slight variation in size is noted in the cysts taken from the same or different fishes. The sporoplasm is large and occupies about one-half of the intrasporal cavity. An iodinophile vacuole is very prominently present in the sporoplasm. Dimensions of spores: length 14-$17\,\mu$, breadth 7-$8\,\mu$, thickness 5.5-$6.5\,\mu$, polar capsules 6-7 by $3\,\mu$.

Henneguya clavicauda n. sp.
(Figs. 31 and 119-125)

HABITAT.—In the subdermal connective tissue of the straw-colored minnow, *Notropis blennius*. From the Rock River near Rockford (June 20, 1927). A single fish, 2.8 cm. long, preserved in formol, showed five cysts on the left side and three on the right side of the body. The whitish cysts were oblong or ellipsoid in form and measured from 1 to 1.5 mm. in the longest diameter.

VEGETATIVE FORM.—In cross-sections the cysts were ellipsoid with their long axis located parallel to the host body surface. The outer surface of the cyst was distinctly outlined. Along the periphery there was a granulated or finely reticulated zone of cytoplasm, about 5 to $10\,\mu$ wide, which was free from nuclei and which in places was radially striated. Internal to this zone, a coarsely vacuolated cytoplasmic area containing nuclei, granules, and disporoblastic pansporoblasts was noted. The remaining part was highly vacuolated and filled with scattered nuclei and spores. Polysporous.

SPORE.—Oval or oblong in front view; broadly spindle-form in side view. The shell is moderately thick. The sutural ridge is prominent, but

sutural line indistinct. Certain spores show three to six thickenings or markings around the posterior half. The characteristic posterior append-age is a single club-shaped body. It measures 20 to 30 μ long, although shorter ones less than 10 μ in length are also met. The anterior end of this appendage expands into a cup-like structure which fits closely the posterior part of the spore. It is circular in cross-section. The append-ages of some spores appear to be composed of a homogeneous substance and possess a smooth surface except the posterior end where a constric-tion often occurs; others are made up of bands of somewhat varying diameters and present a beaded appearance. These conditions are noted both in preserved unstained and in stained spores. The shell and ap-pendage do not show same coloration against same stain. With Giemsa the shell stains blue, the appendage rose-red; with Delafield hematoxylin and eosion, the shell remains almost unstained, while the appendage stains rose-red. Two polar capsules are nearly equal in size and con-vergent. The anterior halves of the capsules are parallel to each other. The sporoplasm contains a very large iodinophile vacuole and two small nuclei. Dimensions of spores: length 10.5-11.5 μ, breadth 8.5-9.5 μ, thick-ness 6 μ, posterior appendage 20-30 μ by 3-6.5 μ, polar capsules 5-5.5 μ by about 2.5 μ, iodinophile vacuole 2-4 μ in diameter.

REMARKS.—There are 52 known species of the genus (Kudo, 1933). Of these *Henneguya macrura* Gurley (Kudo, 1920) shows certain features which resemble those of the present form. Comparison of di-mensions and structure of both the spore and the vegetative form brings out too great a difference to consider them identical.

Henneguya crassicauda n. sp.
(Figs. 32-34 and 126-129)

HABITAT.—In the fins and integument of the stone-roller, *Campo-stoma anomalum*. The fish, 8 cm. long, was collected from a small creek near Rockford (August 18, 1930). The small ovoid cysts on fins were quite conspicuous to the unaided eye, although those on the body surface were visible only through a magnifier.

VEGETATIVE FORM.—In the fin, the seat of infection was the epider-mis or the connective tissue below it. In the body proper, the cysts were situated in the subepidermal connective tissue. The cysts varied from 200 to 400 μ by 100 to 250 μ. The peripheral cytoplasmic zone appeared radially striated—a condition different from that seen in *Henneguya clavicauda* but similar to that observed in *Myxobolus compressus*. The greater portion of the cyst was occupied by spores which were embedded in highly vacuolated cytoplasm. The pansporoblast is disporoblastic. Polysporous.

SPORE.—Oval, oblong, or subcircular in front view; broadly fusiform in side view. The shell is moderately thick and smooth. The sutural line is fairly distinct; the ridge is prominent. There is a characteristic posterior appendage which is independent of the shell. Its anterior end expands into a cup-like form and fits closely the posterior margin of the spore. This condition is similar to that found in *H. clavicauda*. It is broadest at the anterior end and tapers gradually to a bluntly pointed posterior end. It is approximately circular in cross-section at any point. In an unstained spore the appendage is less refractive than that of the last-named species, although distinctly recognizable. In a few spores the appendage was bifurcated. Staining brings about a differentiation between the shell and appendage similar to that stated for the last species. Two polar capsules are large, pyriform, and convergent, extending about to the middle of the intrasporal cavity. The sporoplasm fills the posterior half of the spore and is finely granulated. The iodinophile vacuole is very large and the two nuclei are highly vesicular. Dimensions of spores: length 12-14.5 μ, breadth 8.5-10.5 μ, thickness 6-7 μ, posterior appendage 40-55 μ by 3.5-4.5 μ, polar capsules 5-6 μ by 3-3.5 μ.

Henneguya exilis Kudo
(Figs. 6, 29, and 30)

This myxosporidian was originally described from the gills of the channel cat, *Ictalurus punctatus*, collected from the Rock River at Sterling (Kudo, 1929). Since then the following additional data were obtained.

HABITAT.—Each of the two gill-arches of a channel cat collected from the Sangamon River near Decatur (August 21, 1929) showed six conspicuous cysts, which were subspherical and which measured from 2 to 3 mm. in diameter. Two fishes caught in the Fox River near Dundee (August 13, 1930) had several cysts of this protozoan in the gills (Fig. 6), and two out of twenty-nine fishes examined at a fish market in Havana (August 28, 1930) were also infected by this myxosporidian. Pieces of the integument of two fishes collected from the Kaskaskia River—one near Vandalia (August 17, 1929) and the other near Keysport (August 19, 1929)—contained several circular to irregularly outlined flattened cysts. They were preserved in Zenker's fluid. In the material from one fish 17 cysts were counted, while 12 cysts were observed in that of the other fish. These cysts were creamy white and measured from 1 to 2.5 mm. in diameter. In another fish, 18.5 cm. long, caught in Lake Decatur (August 29, 1929), five cysts were noticed in the integument. These cysts were circular in form and measured 3 to 4 mm. in

diameter. The spores of these integumental forms were indistinguish-able from those of the branchial form.

VEGETATIVE FORM.—No additional information was obtained on the form occurring in the gills other than that which was already reported (Kudo, 1929). In the sectioned integument, it was found that the cysts were located in the subepidermal connective tissue. Observation on the structure of the cysts and morphological detail of the spore agrees very well with the published report. Hence these recent forms are placed under *Henneguya exilis.* All these rivers from which the infected fishes were collected are tributaries of the Mississippi River. Probably this myxosporidian is a common parasite of the channel cat of this river system.

SUMMARY

1. The results of a preliminary study of fishes of Illinois belonging to thirty-five species with reference to their protozoan parasites are pre-sented. These fishes belong to thirteen families, of which Catostomidae, Cyprinidae, and Siluridae were found to be common hosts to histozoic protozoan parasites.

2. An unusual case of Ichthyophthirius infection in carp is noted.

3. Nineteen new species of Myxosporidia are studied and described.

4. Additional information on four known species of Myxosporidia is given.

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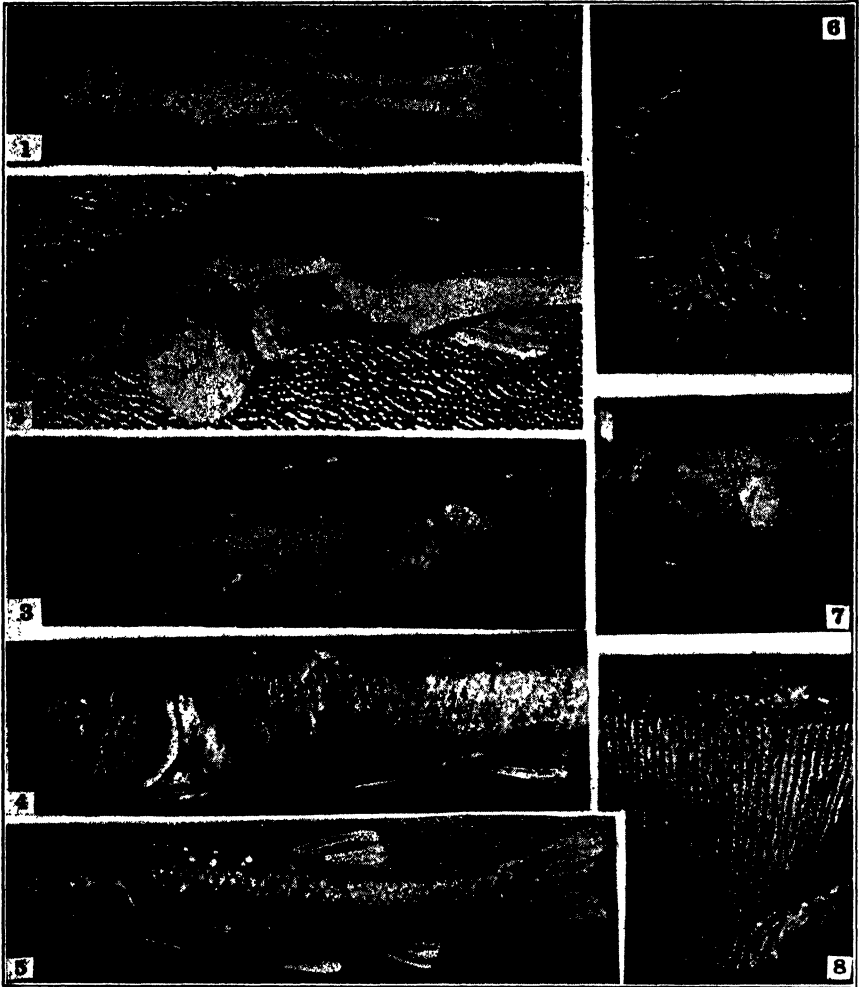
PLATE I

FIG. 1.—Silver-mouthed minnow, *Ericymba buccata,* showing the typical appearance due to a heavy infection of the liver by *Myxosoma grandis.* × 8/10

FIG. 2. — Silver-mouthed minnow with partly exposed viscera, showing the hypertrophied liver infected by *Myxosoma grandis.* × 1.5

FIG. 3. — Trout-perch, *Percopsis guttatus,* with the cysts of *Myxosoma procerum.* × 1

FIG. 4.—Common shiner, *Notropis cornutus,* with a large tumor produced by *Myxosoma robustum.* × 1.5

FIG. 5.—River chub, *Hybopsis kentuckiensis,* with cysts of *Myxobolus squamosus.* × 3/4

FIG. 6.—Gill of a channel catfish, *Ictalurus punctatus,* with cysts of *Henneguya exilis.* × 1.5

FIG. 7.—Part of the anal fin of a white-nosed sucker, *Moxostoma anisurum,* exhibiting a large tumor composed of cysts of *Myxobolus congesticius.* × 1.5

FIG. 8.—Portion of gill of a carp heavily infected by *Ichthyophthirius multifiliis.* × 1.5
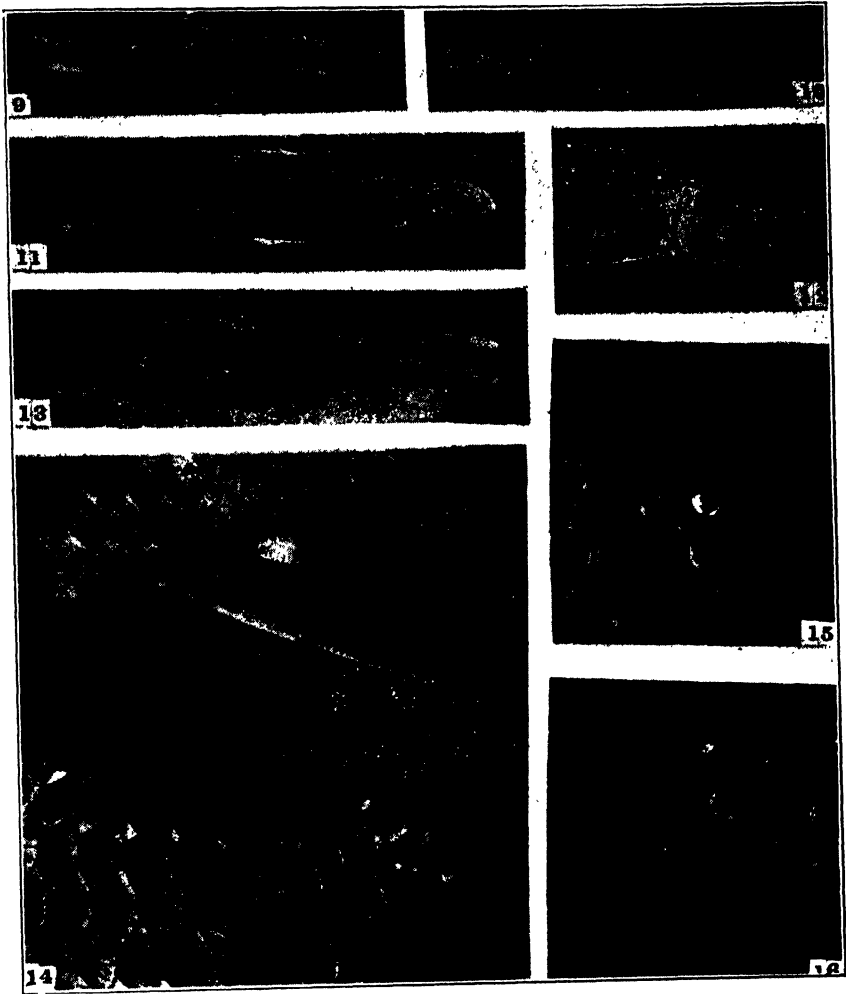
PLATE II

FIG. 9. — Blunt-nosed minnow, *Pimephales notatus*, with numerous cysts of *Myxobolus aureatus* on the fins. × 1.5

FIG. 10.—Bullhead minnow, *Cliola vigilax*, with part of its gill-cover removed, showing cysts of *Myxobolus angustus* in the gills. × 1.5

FIGS. 11 and 12.—Blunt-nosed minnows with the cysts of *Myxobolus mutabilis*. × 1 and × 1.5

FIG. 13.—Straw-colored minnow, *Notropis blennius*, showing the typical appearance of the integument due to a heavy infection by *Myxobolus compressus*. × 1.5

FIG. 14.—Parts of two white-nosed suckers, *Moxostoma anisurum*, showing tumors produced by *Myxobolus congesticius*. The anal fin of the upper fish exhibits the typical appearance of a large tumor, while a smaller one is noticeable at the base of the caudal fin of the lower fish. × 1.5

FIGS. 15 and 16.—Two short-headed red horses, *Moxostoma breviceps*, showing cysts of *Myxobolus conspicuus*. × 1/3
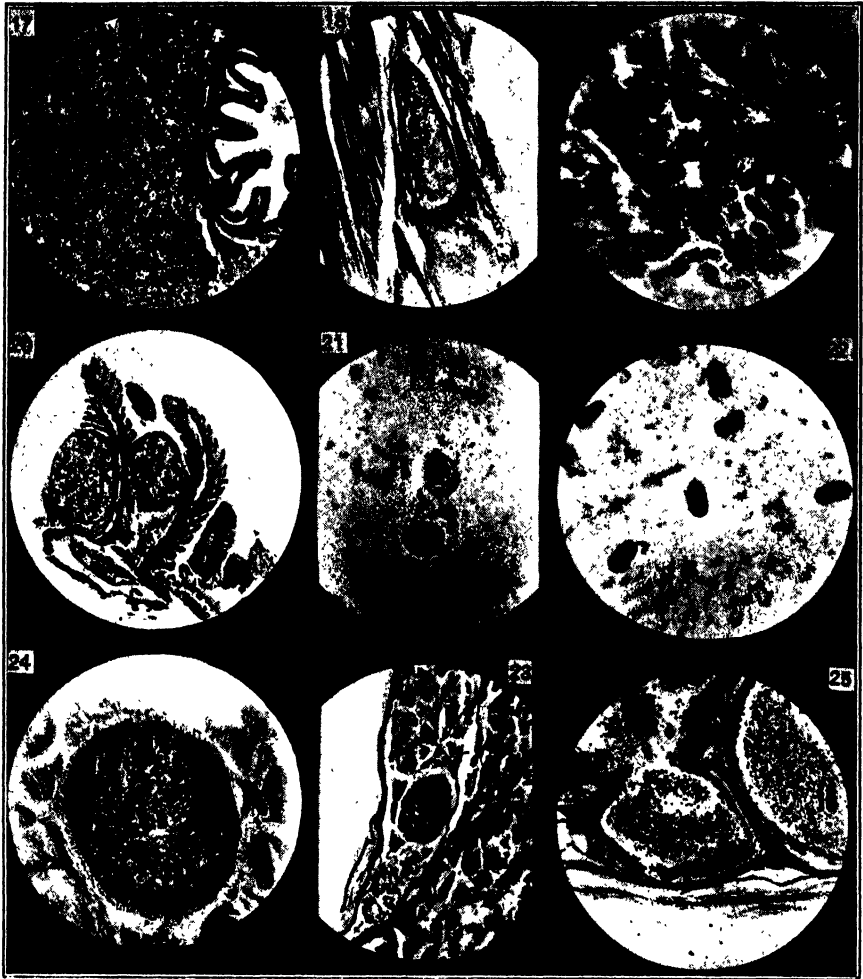
PLATE III

FIG. 17.—Part of a section of the viscera of *Ericymba buccata*, showing its liver heavily infected by *Myxosoma grandis.* × 47

FIG. 18.—Part of a section through the integument and muscles of *Percopsis guttatus*, showing two cysts of *Myxosoma procerum* in the connective tissue. × 47

FIG. 19.—Part of a similar section under higher magnification. × 450

FIG. 20.—Part of gill of *Cliola vigilax* with cysts of *Myxobolus angustus.* × 47

FIG. 21.—Two Giemsa-stained spores of *Myxosoma bibullatum.* × 450

FIG. 22.—Delafield-stained spores of *Myxobolus bellus.* × 450

FIGS. 23 and 24.—Cross-sections of body muscles of *Carpiodes velifer,* showing cysts of *Myxobolus obliquus.* × 95 and × 230.

FIG. 25.—Portion of section of a tumor on the fin of *Moxostoma anisurum,* containing cysts of *Myxobolus congesticius.* × 47
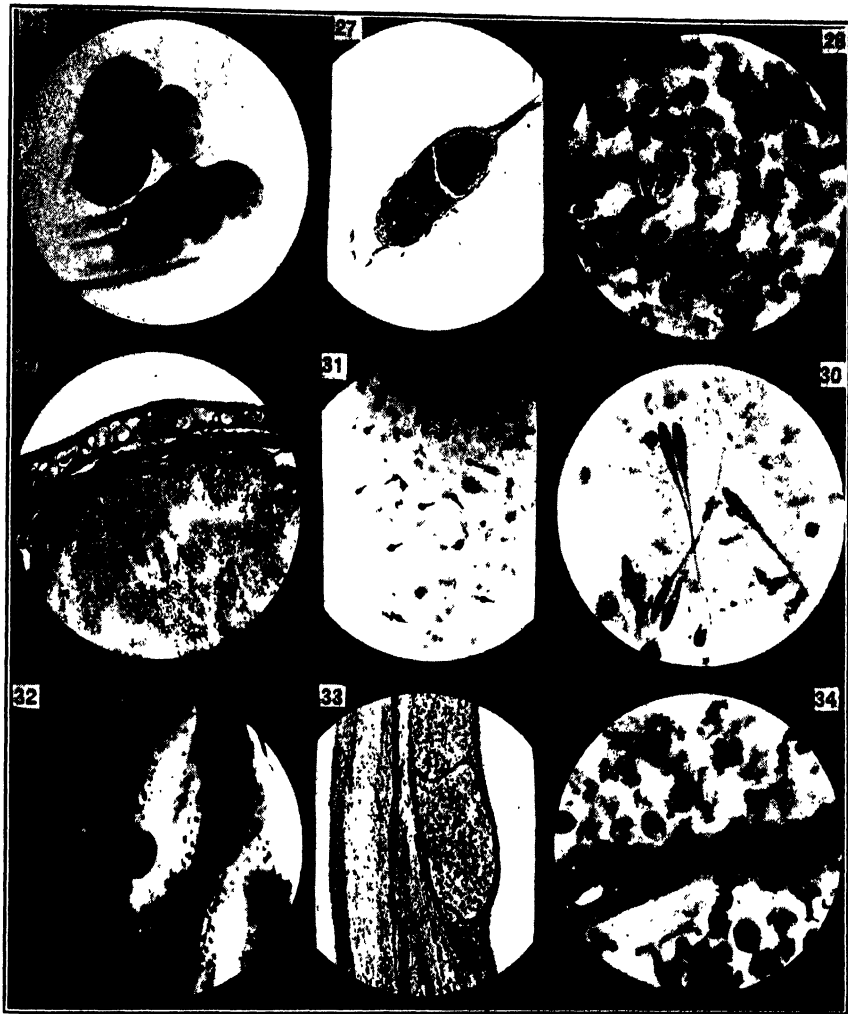
PLATE IV

FIG. 26.—A characteristic view of six cysts of *Myxobolus aureatus* on a pectoral fin of *Pimephales notatus*. × 16

FIGS. 27 and 28.—Cross-sections through cysts of the myxosporidian in a ventral fin of another fish of the same species. × 16 and × 450

FIG. 29.—Part of a section of the integument of *Ictalurus punctatus* with a cyst of *Henneguya exilis*. × 47

FIG. 30.—Stained spores of *Henneguya exilis* in a smear. × 450

FIG. 31.—Stained spores of *H. clavicauda* in a smear. × 95

FIG. 32.—Cysts of *H. crassicauda* in the fin of *Campostoma anomalum*. × 16

FIGS. 33 and 34.—Two cysts of *H. crassicauda* in section. × 47 and × 450
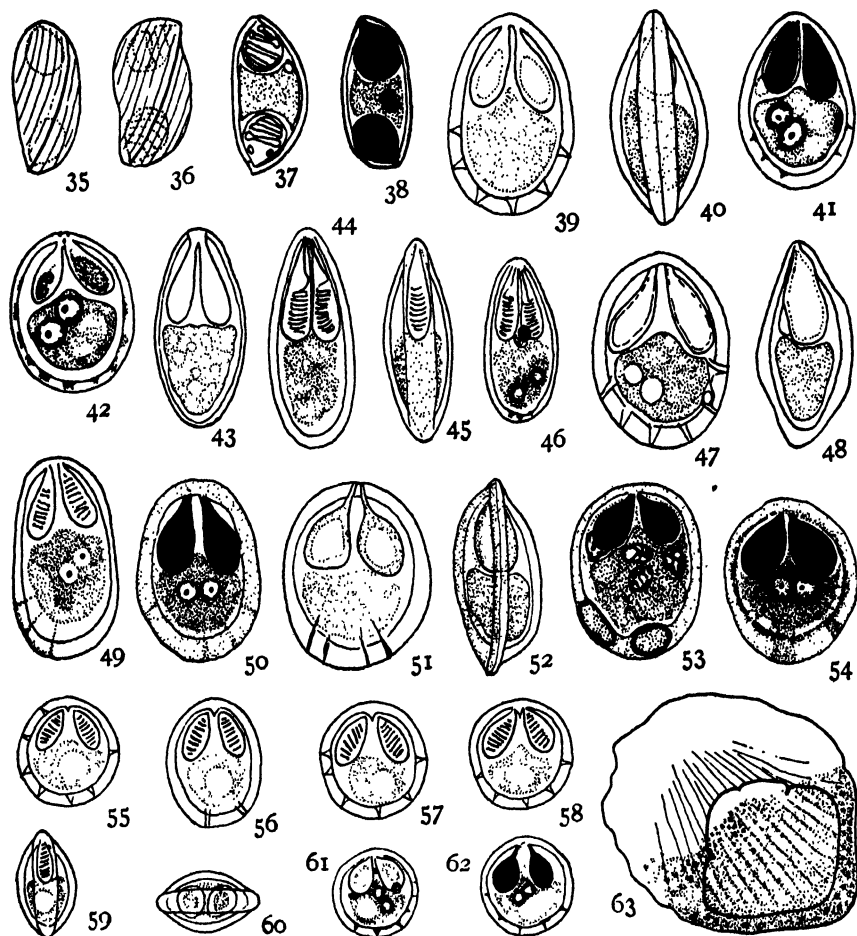
PLATE V

(All figures × 1725, except Fig. 63)

Figs. 35-38.—*Myxidium aplodinoti*: Figs. 35-37, fresh spores; Fig. 38, a Giemsa-stained spore.

Figs. 39-42.—*Myxosoma grandis*: Figs. 39 and 40, preserved spores in front and side views; Figs. 41 and 42, Delafield- and Giemsa-stained spores.

Figs. 43-46.—*Myxosoma procerum*: Figs. 43 and 44, front views of preserved spores; Fig. 45, side view of a preserved spore; Fig. 46, a Delafield-stained spore.

Figs. 47-50.—*Myxosoma robustum*: Fig. 47, front view of a preserved spore; Fig. 48, optical section of a preserved spore from side; Figs. 49 and 50, Heidenhain- and Giemsa-stained spores.

Figs. 51-54.—*Myxosoma bibullatum*: Figs. 51 and 52, front and side views of preserved spores; Fig. 53, a young Giemsa-stained spore, shown in Fig. 21; Fig. 54, a Giemsa-stained spore.

Figs. 55-63.—*Myxobolus squamosus*: Figs. 55-58, front views of preserved spores; Figs. 59 and 60, side and end views of preserved spores; Figs. 61 and 62, Heidenhain- and Giemsa-stained spores; Fig. 63, an infected scale of a river chub (× 10).
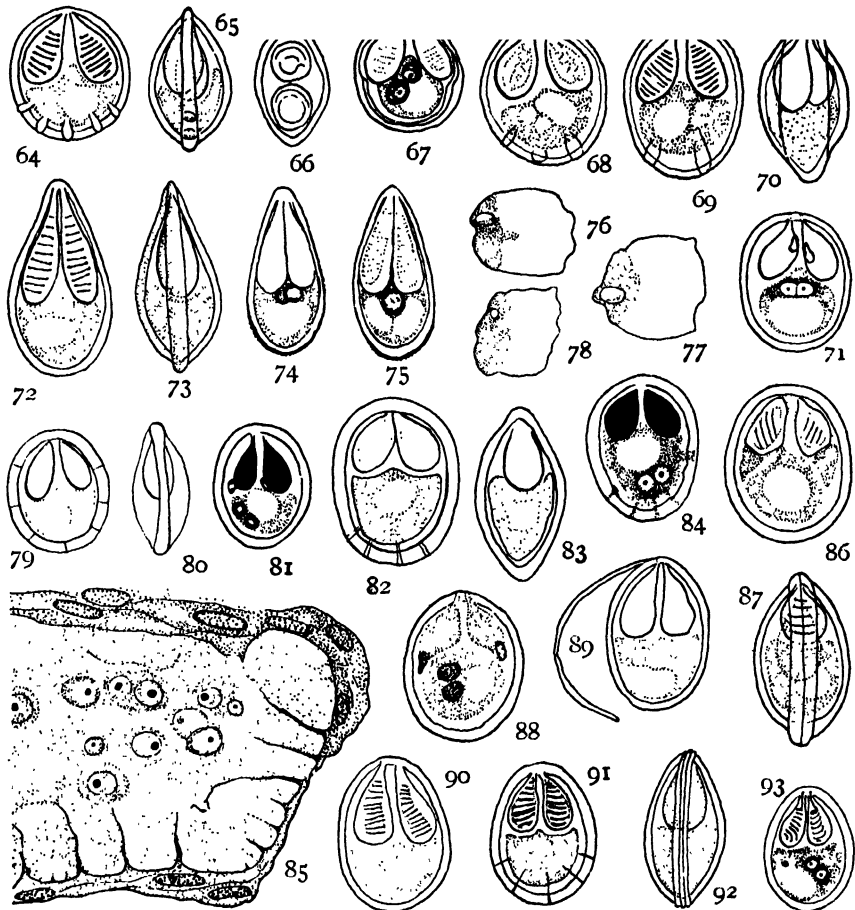
PLATE VI

(All figures × 1725, except Figs. 76-78)

FIGS. 64-67.—*Myxobolus teres*: Figs. 64 and 65, front and side views of preserved spores; Fig. 66, anterior optical section view of a preserved spore; Fig. 67, a Delafield-stained spore.

FIGS. 68-71.—*Myxobolus ovatus*: Figs. 68 and 69, front views of preserved spores; Fig. 70, side view of a preserved spore; Fig. 71, a Delafield-stained spore.

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FIGS. 76-81. — *Myxobolus vastus*: Figs. 76-78, three scales of *Moxostoma aureolum,* each with a cyst of the myxosporidian (× 2/3); Figs. 79 and 80, front and side views of preserved spores; Fig. 81, a Giemsa-stained spore.

FIGS. 82-84.—*Myxobolus gravidus*: Figs. 82 and 83, front and side views of preserved spores; Fig. 84, a Giemsa-stained spore.

FIGS. 85-88.—*Myxobolus compressus*: Fig. 85, part of a section of a cyst and the host tissue; Figs. 86 and 87, front and side views of preserved spores; Fig. 88, a Delafield-stained spore.

FIGS. 89-93. — *Myxobolus mutabilis*: Figs. 89-91, front views of preserved spores; Fig. 92, side view of a preserved spore; Fig. 93, a Heidenhain-stained spore.
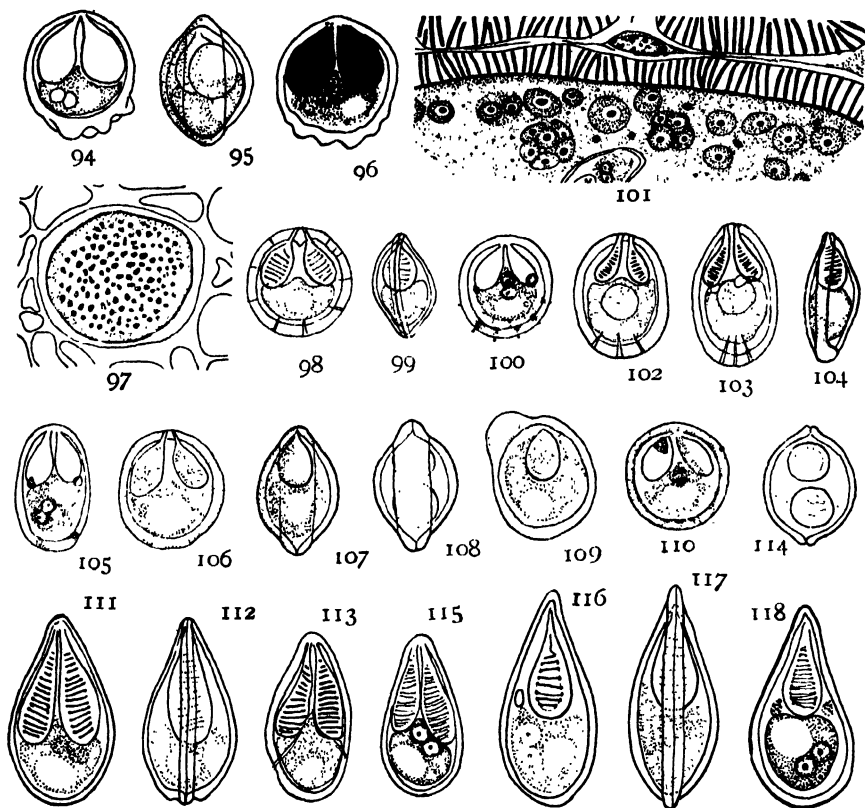
PLATE VII

(All figures × 1725, except Figs. 97 and 101)

FIGS. 94-96.—*Myxobolus nodosus*: Figs. 94 and 95, front and side views of preserved spores; Fig. 96, a Giemsa-stained spore.

FIGS. 97-101.—*Myxobolus obliquus*: Fig. 97, a diagrammatic view of an infected muscle (× 190) ; Figs. 98 and 99, front and side views of preserved spores; Fig. 100, a Delafield-stained spore; Fig. 101, part of a cyst in section (× 1300).

FIGS. 102-105.—*Myxobolus bellus*: Figs. 102 and 103, front views of preserved spores; Fig. 104, side view of a preserved spore; Fig. 105, a Delafield-stained spore.

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FIGS. 111-115.—*Myxobolus aureatus*: Fig. 111-114, preserved spores in different views; Fig. 115, a Delafield-stained spore.

FIGS. 116-118.—*Thelohanellus notatus*: Figs. 116 and 117, preserved spores in front and side views; Fig. 118, a Delafield-stained spore.
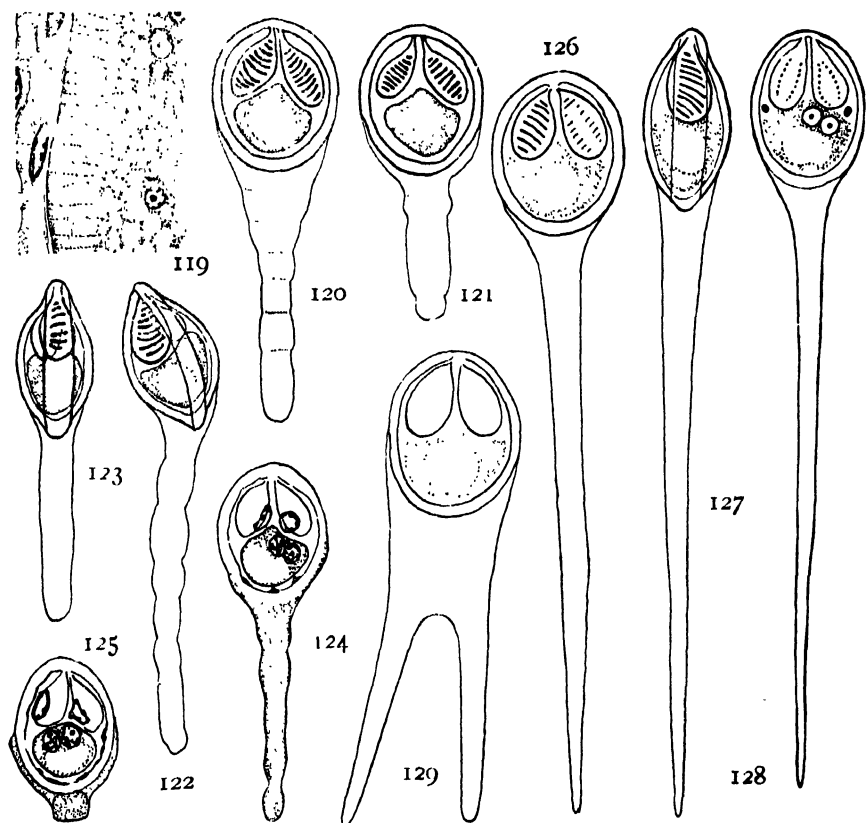
PLATE VIII
(All figures × 1725)

FIGS. 119-125.—*Henneguya clavicauda*: Fig. 119, part of a section of a cyst and the host tissue; Figs. 120 and 121, front views of preserved spores; Figs. 122 and 123, side views of preserved spores; Figs. 124 and 125, Delafield-eosin-stained spores.

FIGS. 126-129. — *Henneguya crassicauda*: Figs. 126 and 127, front and side views of preserved spores; Fig. 128, a Delafield-stained spore; Fig. 129, an abnormal spore with a bifurcated caudal prolongation.

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THE PAPILLOSE ALLOCREADIIDAE

A Study of their Morphology, Life
Histories, and Relationships

WITH FOUR PLATES AND SIX TEXT-FIGURES

BY

SEWELL HEPBURN HOPKINS

CONTENTS

ACKNOWLEDGMENT

INTRODUCTION

The term "papillose Allocreadiidae" as used in this paper refers to all members of the family which are furnished with oral papillae. In the forms considered here the oral papillae are six projections of the oral sucker containing strong muscle fibers like those of the sucker itself; some of the fibers are continuous with those of the sucker wall and run more or less obliquely through the length of the papilla, and others run transversely through the papilla without connecting with fibers in the sucker; the nuclei belonging to the papilla musculature do not lie in the papillae, but in the wall of the sucker at the base of each papilla. Of the six papillae, one pair project laterally from the sucker near the ventral surface and the other four arise from the dorsal wall of the sucker. The structure of the oral papillae is the same in Crepidostomum (which includes the forms previously assigned to Acrolichanus and Stephanophiala), Megalogonia, and Bunodera, and my study has shown that the other morphological features of these genera also indicate a close relationship.

In my analysis of the morphology of these trematodes, I have placed the emphasis on resemblances or differences in the connections and in the histology of organs and parts, rather than on the exact position, size, or shape of the various structures; for a study of abundant specimens and of living material shows that the shape, size, and position of most parts are extremely variable in trematodes because of growth changes, differences in state of contraction of individuals, and other factors discussed later in this paper. I have attempted to work out the life histories and the excretory patterns of as many species as possible in order to determine whether or not the resemblances in type of larva and in type of excretory system agree with the resemblances in the gross morphology of adults on which most of the present conceptions of relationships are based. It is evident from this study that there is need of a revaluation of the importance of the various morphological features of Digenea as indicators of relationship, and that the morphology and biology of the various developmental stages, i.e., the ontogeny, must be taken into consideration before conceptions of the phylogenetic relationships of families, genera, and species of Digenea can have any true value.

The tendency of early helminthologists was to put all papillose distomes together in one group, regardless of other features or even of homologous structure of the papillae. Recently the tendency has been toward increasing separation; the latest general works on trematodes

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(Poche 1926, Fuhrmann 1928) place some of the papillose Allocreadiidae in the sub-family Stephanophialinae Nicoll, distinguished only by the possession of papillae, while Bunodera is placed in a separate family, the Bunoderidae. My analysis of the morphology and ontogeny of the papillose genera and species indicates that Crepidostomum is more closely related to Allocreadium than are some of the genera now included in the Allocreadiinae and that Bunodera and Megalogonia are more closely related to Crepidostomum than some of the genera now included in the Allocreadiidae are related to each other. If the papillae were removed from any species of Crepidostomum it would be very difficult if not im-. possible to distinguish it from Allocreadium. The evidence now available suggests the probability that Allocreadium and Crepidostomum represent offshoots from the same ancestral stem, and that Bunodera and Megalogonia represent offshoots from the Crepidostomum branch of this stem.

MATERIALS AND METHODS

The preserved specimens used in my study were from many different sources, which are indicated in the descriptions of the species. Many specimens were collected by myself; others were borrowed from the collection of Professor Ward, from other investigators, and from American and European museums. Whenever it was possible to obtain enough living specimens of a species the animals were studied alive in order to note their actions and the changes in the shape and position of the various parts as the worms extended and contracted, and the excretory system and finer parts of the reproductive system were traced out. The study of living specimens was found to be far more satisfactory than any treatment of preserved specimens. Many specimens were also mounted in toto or sectioned; reconstructions from serial sections were used as a check on the results of study of living specimens; whole mounts were valuable for measurements, but in most cases were found not to give an adequate idea of the fundamental structure. Living specimens were studied while flattened under a cover slip in physiological salt solution, tap water, distilled water, or horse blood serum; for purposes of measurement some specimens were also studied without flattening. Infection experiments were carried out whenever enough cercariae or metacercariae could be obtained.

In the descriptive section which follows, the genus Crepidostomum and its species will be discussed first, followed by Megalogonia and Bunodera. Under each species the adult is considered first and then an account is given of the life history so far as it is known. Hosts and localities not previously reported are indicated by the asterisk (*).

MORPHOLOGY

GENUS CREPIDOSTOMUM Braun 1900

Since the original setting up of this genus with the two species *C. metoecus* and *C. farionis,* the addition of several more species and the extension of our knowledge of structural features and variations in structure within the genus have made it necessary to revise the generic description. The following diagnosis brings the characterization of Crepidostomum up to date.

Allocreadiidae with six muscular oral papillae projecting from oral sucker, four dorsal and two ventral. Body of adult 0.4 to 6.0 mm. long, width usually about one-fourth length. Oral sucker larger than ventral, ventral larger than oral, or both the same size. Prepharynx, pharynx, and long muscular esophagus present, esophagus often dividing just before running into crura; crural fork anterior or dorsal to ventral sucker; crura running through dorsal half of body nearly to posterior end. Genital pore ventral, median or slightly to one side of median line, between suckers; common genital sinus very small, obliterated when cirrus is everted. Cirrus sac muscular, varying in form and size in different species, reaching only to anterior edge or center of ventral sucker in some and back as far as testes in others; sac always containing seminal vesicle, pars prostatica, strongly muscular cirrus, and prostate glands; anterior end of sac protrusible. Testes two, undivided, with margins entire or slightly lobed, lying near ventral surface between ovary and posterior end of body, either tandem or oblique; vasa efferentia running forward and joining to form short vas deferens which enters posterior end of seminal vesicle. Ovary pear-shaped, near dorsal surface close behind ventral sucker, or dorsal to its posterior margin, sometimes median, more often lateral to median line on either side. Seminal receptacle pear-shaped, near dorsal surface close behind ovary. Oviduct arising from median side of ovary, almost immediately widening to fertilization chamber, receiving seminal duct from seminal receptacle at distal end of fertilization chamber, then running a short distance farther before receiving common vitelline duct, and soon afterwards entering ventral oötype; lumen of oviduct ciliated. Shell glands lying loose in parenchyma, surrounding and opening into oviduct and oötype. Laurer's canal branching off of seminal duct near receptacle and running to pore on dorsal surface usually over intestinal cecum on side farthest from ovary and receptacle. Uterus a narrow tube with thin muscular walls, usually extending back from oötype to anterior margin of anterior testis, but sometimes running back in convoluted course dorsal or lateral to testes as far as posterior edge of posterior testis before turning anteriad; terminal

part of uterus, beginning dorsal to ventral sucker, slightly modified by increased thickness of muscular wall to form metraterm, with or without projections on inner wall. Intrauterine eggs one to several hundred, but usually less than fifty; ovidal or ellipsoidal, 50 to 95 μ long, shell thin, yellowish, operculate; eggs deposited while in single cell stage. Vitellaria mostly lateral and ventral to intestinal crura, from pharynx, from crural fork, or from ventral sucker almost to posterior tip of body, extending into intercrural space between and posterior to testes and anterior to ovary in some species; longitudinal vitelline ducts joined behind posterior testis; transverse ducts meeting near ovary, usually forming vitelline reservoir, from which common vitelline duct runs to oviduct. Excretory bladder an undivided tube or pouch dorsal to testes, from anterior end of which a collecting duct on each side runs to level of ventral sucker and divides into anterior and posterior branch; three groups of flame cells tributary to each of these branches; flame cell formula 2 [(2 + 2 + 2) + (2 + 2 + 2)], perhaps modified in some species by additional divisions of flame cells in some or all groups. A pair of pigmented eyespots present in immature specimens, often persisting throughout life. Miracidium with a pair of fused pigmented eyespots, ciliated over entire surface; cuticular plates lacking; one pair of flame cells present; developing in egg free in water. Redia without ambulatory processes; pharynx large, gut rudimentary, birth pore poorly developed or lacking, flame cells four to 22 or more; developing in liver, gills, or mantle of Sphaeriidae. Cercaria a slender-tailed ophthalmoxiphidiocercaria with about three pairs of cephalic glands and a large number of cystogenous glands. Metacercaria encysted in aquatic insects or crustacea. Adults usually in intestine, sometimes in stomach, pyloric ceca, or gall bladder of freshwater fishes; occasionally in bats, urodeles, and turtles. Type species, *C. metoecus* (Braun 1900).

Crepidostomum farionis (O. F. Müller 1784)

SYNONYMS.—*Fasciola farionis* O. F. Müller 1784; *Fasciola truttae* Froelich 1789; *Distoma laureatum* Zeder 1800; *Fasciola laurcata* (Zeder) Nordmann 1840; *Crossodera laureata* (Zeder) Cobbold 1860; *Distoma farionis* (O. F. Müller) Blanchard 1891; *Crepidostomum laureatum* (Zeder) Braun 1900a; *Stephanophiala laureata* (Zeder) Nicoll 1909; *Stephanophiala transmarina* Nicoll 1909; *Stephanophiala farionis* (O. F. Müller) Faust 1918; *Stephanophiala vitelloba* Faust 1918; *Crepidostomum ussuriense* Layman 1930; *Crepidostomum vitellobum* (Faust) Hopkins 1931a.

HOSTS AND LOCALITIES REPORTED.—*Salmo trutta* Linn. (= *Salmo fario, Trutta trutta, Trutta fario*), Great Britain; Sweden; Denmark;

France; Germany; Russia. *Salmo lacustris,* Finland. **Salmo clarkii,* *Flathead Lake, Montana. *Salmo lewisi* (= *Salmo mykiss, Salmo mykiss lewisi*), Park Co., Montana; Heart Lake and Yellowstone Lake, Yellowstone Park. *Salvelinus alpinus* (= *Salmo salvelinus, Salvelinus salvelinus*), Scandinavia; Germany. *Salvelinus fontinalis,* Canada, (Montreal market) ; *Vermont. *Salvelinus* sp., Peter the Great Bay, Siberia. *Coregonus oxyrhynchus,* Scandinavia; Germany. *Prosopium williamsoni* (*Coregonus williamsoni*), Bitter Root River, Montana. *Thymallus thymallus* (*Thymallus vulgaris*), Great Britain; Scandinavia; Germany. *Stenodus leucichthys,* Russia. *Coregonus lavaretus,* Europe. **Salvelinus malma,* *Jordan Lake at Loring and *Excursion Inlet, Alaska. **Salmo irideus,* *Hatchery Lake at Loring, Alaska. **Salmo mykiss,* Jordan Lake at Loring, Alaska. **Perca fluviatilis,* Vienna, Austria.

This species was first described by O. F. Müller (1784) as *Fasciola farionis.* Froelich (1789) reported as a new species *Fasciola truttae,* but Zeder (1800) compared Froelich's specimens with his own and pronounced them both identical with *Fasciola farionis* O.F.M.; this species Zeder redescribed under the new name *Distoma laurcatum.* It is evident that *D. laurcatum* is merely a synonym of *Crepidostomum farionis* (O.F.M.), although the former name has been used more frequently in the past.

In more modern times *C. farionis* has been described by Olsson (1876), Nicoll (1909), Faust (1918), and Brown (1927). Of these Nicoll has given the most complete description, but his specimens were too few to cover the range of variations in the species, as Odhner (1910) has already remarked. Blanchard (1891) has given a good account of the reproductive system. Faust (1918) and Linton (1893) have given the only descriptions of the American specimens, except for the brief mention of Stafford (1904).

I have studied numerous specimens of *C. farionis* in the collection of Professor Ward, from *Salmo lewisi* in Yellowstone National Park, *Salmo mykiss, Salmo irideus,* and *Salvelinus malma* in Alaska, *Salmo clarkii* in Flathead Lake, Montana, *Salvelinus fontinalis* from Roxbury Hatchery, Vermont, and "Trout" in Frazer River, Colorado. I have compared these American specimens with European specimens of *C. farionis* from *Salmo trutta* (English specimens sent to Professor Ward by Dr. H. A. Baylis) and from *Perca fluviatilis,* Austria (Univ. Berlin Mus. No. 5774), and with the descriptions of European specimens given by Olsson, Blanchard, Odhner, Nicoll, and Brown. It is evident from this study that the only differences existing between the European and the American specimens are of very minor nature and fall well within the range of individual variation. Therefore the name *Stephanophiala transmarina*

Nicoll 1909, proposed for the American form, is a synonym of *Crepidostomum farionis* (O.F.M.), as Faust has already indicated.

Hunninen and Hunter (1933) have described specimens collected by them from trout in New York as *Crepidostomum transmarinum* (Nicoll) and claim that this species is distinct from *C. farionis;* I have examined one of their specimens (8617) and find it identical with *C. farionis.*

Through the courtesy of Professor Faust and Professor Ward I have had the privilege of examining a whole mount, a series of frontal sections, and a series of tranverse sections of Faust's original specimens of *Stephanophiala vitelloba* Faust 1918 (Fig. 10). This species was described from ten specimens found in the gall bladder of *Coregonus williamsoni* from Bitter Root River at Fort Missoula, Montana. Careful examination has shown that Faust's description is wrong in some particulars, the most important of which are corrected, in the following sentences: The esophagus is not especially short, being nearly twice as long as the pharynx. The cirrus sac and its included parts are exactly as in *C. farionis.* The ovary is pear-shaped. Laurer's canal opens on the dorsal surface over one of the intestinal crura. The entire reproductive system agrees with that of *C. farionis,* including the vitellaria which Faust considered the most distinctive feature. Since the size of the body agrees with that of young adults of *C. farionis* and the size of the eggs falls within the range of variation of this species, there is no characteristic left to distinguish Faust's *S. vitelloba* from *C. farionis.* It is evident, therefore, that *Stephanophiala vitelloba* Faust 1918 is a synonym of *Crepidostomum farionis* (O.F.M.), Faust's specimens being young individuals which have only recently reached the egg-forming stage, as I have previously suggested (Hopkins 1931a).

Layman (1930) gives a brief description of a "new species" of Crepidostomum from the intestine of *Salvelinus* sp. in Peter the Great Bay near Vladivostok, Siberia. The figure and all the data given for this form, *Crepidostomum ussuriensis* Layman 1930 (later in the same paper called *C. ussuriense,* which is the correct form grammatically), agree perfectly with *C. farionis,* with which it is almost certainly synonymous. It is of interest to note that Layman describes and figures the cirrus sac as extending posteriorly beyond the ventral sucker to the ovary, as it does in many but not all American specimens.

Layman's report partially fills a great gap in our knowledge of the distribution of *C. farionis.* We now know that this species occurs in Northern and Central Europe, in the Volga River in Russia, in streams and lakes of both the Atlantic and the Pacific watersheds in Northern North America, and on the Pacific coast of Siberia. The present evidence strongly suggests that the distribution of *C. farionis* is co-extensive with

the fresh-water range of salmonoid fishes in the Northern Hemisphere, except where the absence of the invertebrate hosts makes the propagation of the species impossible.

The miracidium of *C. farionis* was described by Willemoes-Suhm (1873), but little is known except that it is ciliated and has a black eyespot; the only individual studied had hatched from the egg after 34 days in water. Brown (1927) has described the other stages in the life cycle. The cercaria, a stylet-bearing cercaria with pigmented eyespots, therefore belonging to Nöller's group Ophthalmoxiphidiocercariae, develops in rediae in *Pisidium amnicum* (Müller) and less frequently in *Sphaerium corneum* (L.). The excretory formula of the cercaria is given as $2[(2+4)+(4+3+3+3)]$; the excretory system of the metacercaria and adult is on the same plan, according to Brown, but he could see only two flame cells in each of the six groups in these stages. The metacercariae were found encysted in the fat bodies and abdominal musculature of a mayfly, *Ephemera danica* (Müller). No infection experiments were reported by Brown. Baylis (1931) has reported the metacercaria of *C. farionis* from the amphipod *Gammarus pulex*. Nothing has been reported on the life history of *C. farionis* outside of Great Britain; in view of the tremendous range of the species, it seems probable that this trematode must be able to adapt itself to other invertebrate hosts in different parts of its range, though probably always remaining dependent on Sphaeriidae for its molluscan host. The ophthalmoxiphidiocercaria (Cercaria X. 4) reported by Harper (1929) may be identical with Brown's cercaria.

SPECIFIC DIAGNOSIS.—Summing up the information now available, the following specific diagnosis may be given for *Crepidostomum farionis:*

With the characters of the genus. Length of sexually mature specimens 1 to 6 mm., body broad and thick, greatest width (in region of ventral sucker) usually one-fourth to one-third of length in preserved specimens. Suckers large, oral sucker about two-thirds as large as ventral sucker. Oral papillae relatively small; ventro-lateral pair slightly larger than the four dorsal papillae, which are approximately equal. Pharynx nearly spherical to elongate-elliptical; length of pharynx one-half to three-fourths diameter of oral sucker. Esophagus sometimes only slightly exceeding length of pharynx, sometimes twice as long, dividing just before passing over into intestinal crura. Crural fork sometimes a little anterior to level of ventral sucker, sometimes dorsal to center of ventral sucker. Common genital pore median or very slightly lateral to median line, ventral to pharynx or just behind this level, some distance anterior to level of crural fork. Cirrus sac elongate-pyriform to sausage-shaped, extending back over ventral sucker, sometimes ending near center

of sucker and sometimes reaching back past sucker as far as level of ovary. Seminal vesicle narrowed to thin duct anteriorly, nearly straight to slightly convoluted, taking up two-fifths to three-fourths length of sac; pars prostatica small; cirrus straight to slightly convoluted, with relatively thin muscular wall. Ovary pear-shaped, slightly lateral or median near dorsal surface just behind ventral sucker or dorsal to its posterior edge. Seminal receptacle pear-shaped, near dorsal surface immediately behind ovary. Laurer's canal opening on dorsal surface just above intestinal cecum on side opposite to seminal receptacle. Vitelline follicles extending along sides of body from pharynx to posterior end of body, lying lateral and ventral to intestinal crura from crural fork to ends of crura and extending inward to median line behind testes, filling in the post-testicular region solidly on the ventral side of the body; few or no follicles dorsal to level of intestinal crura. Uterus usually entirely anterior to testes, sometimes extending back dorsally to level of center of anterior testis; intrauterine eggs 65 to 85 μ long and 40 to 50 μ wide, one to about one hundred in number. Testes tandem, approximately in middle of post-acetabular region or a little farther forward. Excretory bladder a narrow elongate sac or broad tube extending forward as far as anterior edge of anterior testis or posterior edge of ovary, close to dorsal surface; flame cell formula unknown in adult, but pattern same as that of *C. cooperi.* Miracidium with complete coat of cilia and fused pigmented eyespots. Cercaria an ophthalmoxiphidiocercaria developing in rediae in the gills of *Pisidium amnicum* and *Sphaerium corneum.* Metacercaria encysted in abdomen of mayflies (*Ephemera danica*) and in amphipods (*Gammaruus pulex*). Adult in intestine of fresh-water Salmonidae, rarely in other fishes.

Crepidostomum metoecus (Braun 1900)

SYNONYMS.—*Distomum metoecus* Braun 1900, *Crepidostomum succicum* Nybelin 1932.

HOSTS AND LOCALITIES REPORTED. — *Nyctalus noctula* (Schreber) (*Vespertilio noctula, V. noctua*), Europe. *Nyctalus maximus* (Fatio) (*Vespertilio lasiopterus*), Europe. (Braun does not state where the specimens in the Vienna museum were collected, but both of these bats are Central European species according to Brohmer (1929) in "Die Tierwelt Mitteleuropas.") **Perca fluviatilis,* Vienna, Austria. The following were reported as hosts of *C. suecicum* by Nybelin (1932): *Thymallus thymallus,* Sweden; *Salmo trutta,* Sweden; *Lota lota,* Sweden; *Cottus gobio,* Sweden; *Salmo alpinus,* Sweden.

This˜ species was first described by Braun (1900). Later Braun (1900a) published a more complete description and founded the genus

Crepidostomum with *C. metoecus* as type. In this paper he corrected some of the statements made in the first description and gave a fairly good figure. Odhner (1905, 1910) made some further corrections and additions after studying Braun's original specimens. Braun found his specimens in vials in the Vienna museum labeled as from the two species of bats named above, and *C. metoecus* has always since then been considered a parasite of bats; however, it has never been reported from bats since the original discovery, and until now has been known only from the type material.

Recently Nybelin (1932) has described a new species, *Crepidostomum succicum*, from Swedish fresh-water fishes, *Thymallus thymallus, Salmo trutta, Lota lota, Cottus gobio,* and *Salmo alpinus.* The specimens from *Salmo alpinus*, as described and figured by Nybelin, look very much like young specimens of *Crepidostomum farionis* except for their extremely small size (0.49 to 0.92 mm. long); the other specimens seem to me to be specifically identical with specimens from *Perca fluviatilis* which I found in one of the vials of parasites loaned to Professor Ward by the University of Berlin Zoological Museum (labeled *"Distoma nodulosum* Zed.—*Perca fluviatilis*—Wien—5774. Samml. Mehlis No. 87"). Seven of these specimens were found to agree perfectly (except for more elongated form and greater number of eggs) with two of Braun's original specimens from *Nyctalus noctula* which were loaned to Professor Ward by the Vienna Naturhistorisches Museum. There were also 12 specimens of *C. farionis* in the same vial from *Perca fluviatilis.* There is now scarcely a doubt in my mind that Nybelin's specimens and those from *Perca fluviatilis* are specifically identical with Braun's specimens from bats; I therefore consider *Crepidostomum succicum* Nybelin 1932 a synonym of *C. metoecus* (Braun). It is noteworthy that Nybelin's specimens and those from Perca contained many more eggs than the specimens from bats (8 to 24 eggs are shown in Nybelin's figures; I found up to 15 eggs in the specimens from Perca; Braun found only one or two eggs in his specimens); this fact, together with the abundance in fish and the apparent rarity in bats, makes it seem most probable that fish are the "natural hosts" of *C. metoecus* and that bats are only "occasional" or "accidental" hosts.

The two "type" specimens from bats which I studied gave the following measurements; one (Fig. 11), which was somewhat contracted but fairly straight, was 0.88 mm. long, 0.24 mm. wide at widest point (level of anterior testis), with oral sucker 0.13 by 0.11 mm., ventral sucker 0.13 by 0.14 mm., and the single egg 60 by 35 μ; the other specimen was contracted and the anterior end was bent strongly ventrad, making the apparent length only 0.73 mm.; no accurate measurements

could be made on the latter specimen, which appeared to contain only one egg. The genital pore is posterior to the level of the crural fork, as shown by Braun, and the cirrus sac turns ventrad after reaching back past the ventral sucker. The testes are very large, round, and in tandem position; they fill up the greater part of the post-acetabular region and reach nearly to the posterior end of the body. The vitelline follicles reach from oral sucker to posterior end and are mostly lateral and ventral to the intestinal crura, but also extend all the way to the dorsal surface anterior to the ovary and behind the posterior testis. The oral papillae are exactly the same shape and arrangement as in *C. cooperi*. The body is widest in the region of the testes. The ventral sucker projects a little. The other features are shown in Figs. 12 and 13.

The seven specimens of *C. metoecus* from *Perca fluviatilis* range from 1.0 to 1.22 mm. in length and from 0.17 to 0.25 mm. in width. The diameter of the oral sucker is 0.10 to 0.17 mm., and that of the ventral sucker the same. The body is widest at or near the level of the ovary in all. Except in one specimen, the anterior end of the cirrus sac is protruded and extends 0.10 to 0.20 mm. outside of the body. The genital pore is behind the level of the crural fork. The cirrus sac extends back past the level of the ventral sucker. The ovary lies close to the dorsal surface, to one side of the median line, a short distance behind the ventral sucker; the seminal receptacle lies just behind the ovary. The testes are large, tandem, and vary considerably in size and shape as in other species of the genus; they lie close to the ventral surface. The excretory bladder is an undivided sac lying close to the dorsal surface and ending over the anterior testis. The strong development of the vitellaria, which cover the sides of the body from pharynx to posterior end and also fill in nearly all the space between the other organs, is the most characteristic feature of these specimens; the same distribution of vitellaria is shown by the Vienna museum specimens from the bat and in Nybelin's figures. The eggs in the Perca specimens are about 54 by 33 μ. Most of the structural features are shown fairly well in Figs. 12 and 13.

SPECIFIC DIAGNOSIS.—Combining all the data now available, i.e., Braun's, Odhner's, Nybelin's and my own, the following specific diagnosis of *C. metoecus* may be given:

With the characters of the genus. Length of egg-producing adults from about 0.5 to about 2.7 mm.; width one-fourth to one-tenth length; greatest width between ventral sucker and posterior testis; depth of body slightly less than width. Suckers approximately equal. Oral papillae not notched at tip. Pharynx ovoidal or ellipsoidal, one-third to one-half as long as oral sucker. Esophagus slightly longer than pharynx, much curved in contracted specimens. Crural fork anterior to ventral sucker;

crura running back through dorsal half of body on each side of ventral sucker and gonads, ending a little over half-way between posterior testis and posterior end of body. Genital pore median ventral, posterior to crural fork. Cirrus sac elongated, extending back over ventral sucker and then bending ventrad, often reaching as far as level of ovary; anterior end protrusible. Cirrus relatively long, reaching back about half the length of the cirrus sac, separated from seminal vesicle by small spherical pars prostatica; seminal vesicle not narrowed distally. Ovary pyriform, lateral and dorsal behind ventral sucker, on either right or left side; sometimes at level of posterior edge of ventral sucker, sometimes some distance behind it. Testes large, spherical or ellipsoidal, tandem in median line, about equally far from ventral sucker and posterior end of body. Uterus reaching back to anterior edge of anterior testis (or possibly in some as far as posterior testis?), then curving anteriad. Intrauterine eggs one to twenty-four in specimens observed so far, 53 to 66 μ long, 30 to 45 μ wide. Vitellaria very strongly developed; follicles extending anteriorly as far as pharynx in well-extended specimens and to oral sucker in contracted specimens, and posteriorly as far as posterior tip of body; mostly lateral and ventral to intestinal crura, but follicles also overlapping crura on dorsal side and extending to dorsal surface throughout most of the body length, sometimes meeting in median line anterior to ventral sucker and between testes; apparently always meeting in median line behind testes, where follicles pack the posterior end of the body solidly except for the narrow space occupied by the excretory bladder near the dorsal surface. Excretory bladder an undivided sac extending forward just under the dorsal surface and ending dorsal to the anterior testis; excretory pattern and flame cell formula unknown. Adults in intestine and pyloric ceca of fresh-water fishes and in intestine of bats, Central and Northern Europe.

Nöller (1925) described a new cercaria, *Cercaria arhopalocerca,* which he later (1928) assigned to *Crepidostomum metoecus.* He proposes for all distome cercariae with stylet and eyespots the new group name Ophthalmoxiphidiocercariae, into which may be placed the cercariae of *Allocreadium isoporum* and of all species of Crepidostomum, so far as known. Nöller's cercaria, which develops in rediae in *Pisidium personatum* (in Thuringia), agrees well with the cercaria of *C. cooperi;* his rediae also closely resemble the rediae of this species. The assignment of *Cercaria arhopalocerca* to *C. metoecus* is based on (1) the close resemblance of the cercaria to the cercaria of *C. farionis* as described by Brown (1927) and (2) the complete absence of fish in the spring in which the infested Pisidia were found, as well as the absence of other vertebrates which might serve as hosts for the adults. Nöller obtained metacercariae

by experimental infestation of Chironomus and Corethra larvae, but they were not described; no further experiments were made and there is no evidence that *C. metoecus* occurs in the vicinity, either in bats or in fish. I am inclined to believe that Nöller's cercaria probably does belong to *C. metoecus*, or at least to some species of Crepidostomum, but the present evidence is far from convincing.

In connection with the occurrence of *C. metoecus* in bats and the supposed occurrence of its redia and cercaria in a spring uninhabited by fish, the following suggestion may be offered. It is possible that *C. metoecus* becomes sexually mature in the second intermediate host, as *C. cornutum* and several other Allocreadiidae are known to do. If this is true, the bats reported as hosts may merely have eaten progenetic metacercariae which were already producing eggs. Sexually mature *C. metoecus* (or perhaps *C. farionis*, for that matter) encysted in flying insects such as mayflies might be carried from one stream or pond to another close by, and after the death of the insect host the eggs of the encysted worm might be released into the water, thus giving rise to infestation of the Sphaeriidae in the immediate vicinity.

Crepidostomum cooperi Hopkins 1931

SYNONYMS.—*Crepidostomum ambloplitis* Hopkins 1931; *Crepidostomum solidum* Van Cleave and Mueller 1932; *Crepidostomum fausti* Hunninen and Hunter 1933.

HOSTS AND LOCALITIES REPORTED.—*Perca flavescens*, Go-Home Bay, Ontario; Oneida Lake, New York; *Sebago Lake, Maine. *Ambloplites rupestris*, Go-Home Bay, Ontario; *St. Lawrence River, New York. *Lepomis cyanellus*, *Sangamon River and *Salt Fork River basin, Champaign County, Illinois. *Lepomis humilis*, Sangamon River and Salt Fork River basin, Champaign County, Illinois. *Lepomis megalotis*, Sangamon River and Salt Fork River basin, Champaign County, Illinois. *Lepomis sp.*, *Baton Rouge, Louisiana. *Micropterus salmoides*, *Money, Mississippi (Tallahatchie River). *Eupomotis gibbosus*, Ragged Lake and Barnum Pond, Franklin County, New York. "Catfish," Baton Rouge, Louisiana. *Ameiurus melas*, Salt Fork River basin, Champaign County, Illinois. *Ameiurus natalis*, Salt Fork River basin, Champaign County, Illinois. *Ameiurus nebulosus*, Oneida Lake, New York. *Schilbeodes gyrinus*, experimental infestation. *Schilbeodes miurus*, experimental infestation. *Amyda mutica*, *Blue River, Connorville, Oklahoma.

This species was first described (Hopkins 1931a) from specimens collected by A. R. Cooper at Go-Home Bay and previously listed by Cooper (1915) under the name of *Crepidostomum laureatum* (Zeder). In the same paper I described *Crepidostomum ambloplitis*. A few weeks

later Van Cleave and Mueller (1932) described a new species, *Crepidostomum solidum;* in a footnote they stated that it was their opinion that *Crepidostomum ambloplitis* and *C. cooperi* were variants of the same species, and that both *C. ambloplitis* and *C. solidum* were synonyms of *C. cooperi.* Through the courtesy of Dr. Van Cleave I have been able to examine many of the specimens on which Van Cleave and Mueller's description was based, and found that most of their specimens resemble the *C. ambloplitis* type, but some show resemblances to the *C. cooperi* type. Later I collected specimens from catfish which more completely bridged the gap between these types, leaving no morphological differences on which a specific distinction could be based; therefore I accept the view that *C. ambloplitis* and *C. solidum* are synonyms of *Crepidostomum cooperi.*

Crepidostomum fausti Hunninen and Hunter 1933, from trout, is a synonym of *C. cooperi.* I studied the type specimen of *C. fausti* (U.S.N.M. No. 8615) and paratype (U.S.N.M. No. 8616) and could find nothing to distinguish the species; the authors were misled by lack of knowledge of the variability of *C. cooperi.* Hunninen and Hunter's suggestion that some of the specimens described as *C. laureatum* or *C. farionis* by Linton and by Faust belonged to their species is a speculation with little or no foundation.

The material used in my study of this species consists mostly of specimens collected from sunfish, *Lepomis* spp., in Champaign County, Illinois, and specimens obtained from sunfish and catfish, *Schilbeodes* spp., as a result of experimental feeding with mayfly nymphs containing the metacercaria. In addition I have studied specimens from *Ameiurus* sp., Champaign County, Ill., *Lepomis* sp. and catfish, Baton Rouge, La., *Micropterus salmoides,* Tallahatchie River, Miss. (Simer's specimens), *Ambloplites rupestris* and *Eupomotis gibbosus,* New York, and *Amyda mutica,* Blue River, Oklahoma. The last mentioned lot of specimens is the first reported occurrence of any Crepidostomum in a reptile; it is possible that infestation resulted from the eating of an infested fish. Having an abundance of live material I was able to work out the excretory system and the details of the reproductive system from living specimens. In addition to this method of study, which is by far the best, I have studied whole mounts and serial sections.

SPECIFIC DIAGNOSIS.—The information obtained in this study is summarized in the following specific diagnosis of *Crepidostomum cooperi.*

With the characters of the genus. Sexually mature specimens from about 0.40 to about 1.5 mm. in length; width varying from about one-seventh to about one-half of length according to state of contraction, averaging about one-fourth; depth varying from one-ninth to one-fourth

of length according to state of contraction; greatest width at level of ventral sucker or anterior testis. Ventral sucker one-fifth to one-half body length from anterior end according to size and state of contraction; usually slightly smaller than oral sucker, but sometimes equalling or even exceeding it in contracted specimens. Oral papillae all practically equal in size; ventral pair projecting from lateral margin of oral sucker, either directly laterad or slightly dorsad, not overlapping any part of ventral face of sucker; four dorsal papillae usually attached on transverse equator of dorsal face of sucker, but occasionally near enough to anterior margin to project anteriad beyond it; in life all papillae extend, contract,
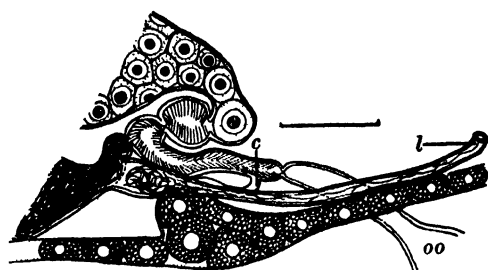
TEXT-FIG. 1.—Female reproductive organs of *C. cooperi*, drawn from living specimen, dorsal view; scale line represents 0.05 mm.; *c*, common vitelline duct; *l*, Laurer's canal; *oo*, oötype

and bend in all directions. Pharynx ovoidal or ellipsoidal, length one-third to one-half, but usually two-fifths, of length of oral sucker. Esophagus two or three times length of pharynx but much convoluted in contracted specimens so that apparent length is less.

Genital pore usually posterior but occasionally in strongly contracted specimens ventral to crural fork; very small common genital atrium obliterated when cirrus sac is everted. Cirrus sac long and slender, tapering from near posterior end to anterior end, reaching back over ventral sucker to level of ovary or sometimes beyond, and rarely as far as posterior testis; varying from nearly straight to considerably convoluted; wall thin but muscular. Seminal vesicle two to four times as long as cirrus but so much convoluted that it occupies only two-thirds to three-fourths length of sac, tapering toward anterior end, often divided by a constriction into large posterior and small anterior chamber. Pars prostatica large, ovoidal or ellipsoidal. Cirrus slender, convoluted, with rather thin but muscular wall; lumen smooth-walled. Testes close together near ventral surface in posterior half of body, extremely variable in size and shape; twice as long as wide, spherical, or twice as wide as long according to state of contraction of body; distance from posterior testis to

posterior end one-tenth to one-fourth body length, varying according to relative size of testes and degree of contraction or extension of body. Ovary pear-shaped, dorsal, close behind and usually overlapping ventral sucker, median or slightly lateral on either side. Seminal receptacle of extremely variable size close to posterior margin of ovary. Laurer's canal running to pore on dorsal surface above intestinal cecum of opposite side. Uterus increasing in length and convolutions with age; running almost straight forward in immature specimens, back as far as anterior testis in most individuals, and back as far as center of posterior testis in a few (Simer's specimens from Micropterus); wall thin but fairly muscular; metraterm with thicker and more muscular wall beginning near posterior edge of ventral sucker, with smooth-walled lumen. Intrauterine eggs few, up to about 40; size ranging in different lots of preserved specimens from 50 to 60 μ by 30 to 40 μ, from 56 to 65 μ by 35 to 45 μ, and from 60 to 75 μ by 40 to 55 μ, and in living unflattened specimens from 62 to 75 μ by 42 to 55 μ; shells thin, yellowish, operculate. Spermatozoa about 120 μ long, with rod-shaped head 15 to 20 μ long and very slender tail. Vitellaria extending from near posterior end to about half-way between pharynx and ventral sucker, sometimes reaching posterior end of oral sucker in strongly contracted specimens (Figs. 2, 3); longitudinal vitelline ducts uniting behind posterior testis; follicles lateral and ventral to intestinal crura from center of ventral

TEXT-FIG. 2.—Excretory system of *C. cooperi* adult.

sucker to posterior testis, lateral, ventral and dorsal to esophagus and crura anterior to ventral sucker; lateral and dorsal to crura and extending clear across ventral surface behind posterior testis; a few follicles also lying median to crura between and in front of testes and above and in front of ventral sucker.

Excretory bladder (Text-fig. 2) a narrow sac or broad tube close to dorsal surface, reaching forward to between anterior and posterior

edge of anterior testis; flame cell formula 2[(2 + 2 + 2) + (2 + 2 + 2)],
vibratile organelle of flame cells about 15 μ long and 5 μ wide (in im-
mature specimens just before attaining female maturity).

Pigmented eyespots, one on each side of pharynx or esophagus,
usually present in adults, compact in some and dispersed in others.

MIRACIDIUM.—The egg cell does not undergo cleavage while within
the uterus, and apparently not even after being ejected into the intestine
of the host, but eggs put into pond water or tap water in a watch glass or
shallow open dish soon begin cleavage; a spherical mass of cells without
structure is formed in 3 days, an ovoidal embryo with two separate pig-
mented eyespots in 5 days, and an apparently mature miracidium in 7
days; however, the external cilia do not become active until shortly before
hatching, which begins in about 10 days (Fig. 4). These results were
obtained at room temperature in summer. The miracidium is pear-shaped,
slightly flattened dorso-ventrally, and is about 65 μ long, 30 to 35 μ wide,
and 25 to 35 μ deep while still in the shell. The cuticula is not divided
into plates, but is completely covered with cilia nearly 10 μ long arranged
in close-set longitudinal rows. The pear-shaped rudimentary gut opens
at the tip of the conical inversible papilla at the anterior end of the body,
and reaches back one-fourth to one-third the body length. Dorsal to or
just behind the posterior end of the gut is a large pigment spot in the
form of two shallow cups fused at their convex surfaces, forming a mass
which appears V-shaped in dorsal or ventral view and round in lateral
·view (Fig. 4). The nerve mass lies ventral to the eyespots. Two large
active flame cells lie one on each side of the body near the dorsal sur-
face and about in the middle of the body length; they are of the same
shape as in the young adults, but smaller, the vibratile organelle being
7 to 9 μ by 3 to 5 μ. The posterior two-thirds of the body is filled with
germ cells.

REDIA.—The redia of *C. cooperi* was found in 65 of 96 *Musculium
transversum* (Say) collected in an oxbow pond formed by the dredging
of Spoon River near St. Joseph, Ill., in collections made from October
8, 1931, to June 9, 1932. The infestation in this period was 67.6%. In
June and July nearly all the large Sphaeriids were dead, but during July
I found 18 adult Musculium; none of these were infested. The redia
was also found in 2 of 3 *M. transversum* and in a single *Pisidium* sp.
collected in July from Sangamon River. *Sphaerium notatum* Sterki was
abundant in the Spoon River oxbow, but 60 of these were examined with
completely negative results.

Each infested Musculium contains rediae of a great variety of forms,
·some slender and active, some very large and looking like sausage-
shaped sporocysts, and some nearly spherical. Some of these are evi-
dently growth stages of the same type of individual, while others are

apparently abnormal. There seems to be no regular order of mother and daughter rediae, for there is no constant difference between rediae containing cercariae and those producing rediae; in fact, frequently the same parent individual contains both rediae and cercariae. There are no ambulatory processes.

Individuals with eyespots, rare in comparison to the others, may constitute a distinct generation (Fig. 5). These are slender, active rediae 0.18 to 0.36 mm. long and 0.05 to 0.07 mm. wide, with a nearly spherical pharynx about 30 μ in diameter. The posterior tip is apparently adhesive, and is used for attachment while the body is pushed forward by extension, as in some rotifers. The anterior end can be inverted so that it serves as a sucker. The gut is small and does not increase as the body grows, so that it becomes proportionately smaller; apparently it disappears when the redia becomes mature. Around the pharynx are 6 gland cells with short ducts opening into the prepharyngeal invagination. I have seen one eyespotted redia, 0.37 by 0.15 mm., which contained immature cercariae; all others contained only very small germ balls. The excretory system of the eyespotted rediae was not studied in any detail. The pigmented eyespot is like that of the miracidium, but more irregular in shape; it lies near the posterior end of the pharynx. It seems probable that the eyespotted rediae develop directly from the miracidium; i.e., they are the same individuals in a more advanced stage of development.

Rediae without eyespots range from slender forms like the eyespotted type to stout sausage-shaped rediae containing young rediae, mature cercariae, or both (Figs. 6, 9). The young rediae just after leaving the parent are 0.12 to 0.25 mm. long according to the phase of contraction and extension. They usually become about 0.6 mm. long before the germ balls develop into mature cercariae, but a few nearly spherical rediae contain cercariae when only 0.3 mm. long. As a redia matures it becomes thicker and loses its motility. Some mature rediae reach a length of 2.0 mm. and most are over 1.0 mm. The gut disappears when the slender motile stage is passed, and in very old rediae the pharynx degenerates and may disappear entirely. No birth pore could be found. The pharynx varies from 21 by 21 μ to 45 by 35 μ, averaging 32 by 29 μ; there is no evidence that it increases in size after the young rediae leave the parent, small rediae having as large a pharynx as large ones. The excretory system consists of a pair of small lateral vesicles in the middle third of the body length with a tube running anteriad and another running posteriad from each; the tubes branch, and the branches divide again into capillaries, but the capillaries and flame cells have not been traced out completely. The number of flame cells varies from 4 in the youngest to 22 in the oldest; in young rediae they are of the same size and shape as in miracidium, but in mature rediae they become much larger and

broader, finally becoming fan-shaped or "toadstool-shaped" like some of the flame cells figured by Looss (1894) for adult trematodes. The smallest flame cells have a vibratile organelle 6 μ long and 2 μ wide, while the largest are 11 μ long and 33 μ wide.

Most of the young motile rediae are found in the spaces between the inner and outer layers of the gills and mantle, where they may be seen pushing their way slowly along. Many of these are only 0.15 to 0.18 mm. long, so they evidently migrate to the gills and mantle very soon after birth. All the mature rediae are found in the liver (digestive gland); the rediae in the gills and mantle contain only very small germ balls. As many as 160 mature rediae have been found in the liver of a single Musculium; the immature rediae are much less numerous. One Musculium isolated in the laboratory from December 8, 1931, to February 9, 1932, contained only 12 rediae, all immature and without eyespots; as there was no chance for infestation during this time the rediae must have been the descendants (probably of the first or second filial generation) of a miracidium which had entered the host at least two months before.

CERCARIA.—The cercaria (Fig. 7) is unpigmented and transparent. The average length at rest is about 300 μ, with width and depth about 100 μ, but a creeping cercaria may vary in length from 150 to 450 μ as it contracts and extends the body. The tail is long and slender, without fins or other modifications, and tapers gradually to a sharp tip; it is .usually slightly longer than the body, averaging about 370 μ long in slightly flattened living specimens. The two suckers are slightly unequal, the oral sucker averaging about 59 by 49 μ and the ventral sucker 44 by 44 μ; the ventral sucker is usually just posterior to the middle of the body, but its position varies greatly with the changes in body shape. Both suckers are fringed with crowns of sticky protruberances which project from the outside rim when the sucker is everted or flattened against a surface, and are withdrawn into the cavity when the sucker is drawn in or contracted; this fringe is inconspicuous on the oral sucker but large on the ventral sucker.

The stylet (Fig. 8a) lies near the anterior tip of the body with its base imbedded in a pit in the dorsal wall of the oral sucker; its length is about 25 μ. Two large conspicuous eyespots lie just below the dorsal surface lateral to the pharynx or a little behind this level; they are shallow cups of small elliptical brown granules which look black *en masse*; each cup is about 15 μ in diameter. Three large cephalic gland cells lie on each side of the ventral sucker, but somewhat anterior to it in extended specimens. Two of the glands give rise to ducts which run along the lateral margin of the body, while the duct from the other gland

runs forward near the median line; all of the ducts open through pores on the dorsal surface near the stylet. The gland cells are either pear-shaped or lobate; their finely granular, slightly refractive contents take only a faint yellowish tinge when treated with neutral red in life; each cell is 30 to 45 μ long by 15 to 25 μ, with a nucleus 7 to 9 μ in diameter. Forty to fifty cystogenous glands (Fig. 7) lie just below the dorsal surface from about half-way between pharynx and oral sucker to the posterior end of the body; they are each about 15 to 22 μ in diameter, with a nucleus about 5 μ in diameter; the cell contents are hyaline but take a very bright orange-red stain with neutral red in life.

The prepharynx is very narrow and about 45 to 60 μ long. The small ellipsoidal pharynx is about 18 μ long and 15 μ in diameter. A narrow, indistinct esophagus runs back nearly to the ventral sucker and divides into two short rudimentary crura, which do not extend past the level of the ventral sucker and sometimes seem to be lacking entirely.

The female reproductive complex is represented by a bilobed mass of small deep-staining cells dorsal to or just behind the posterior edge of the ventral sucker. Two strands of similar cells can sometimes be seen running anteriad over the sucker and joining just in front of it. The testes are represented by two discoidal groups of deep-staining cells lying in a tandem position close to the ventral surface in about the middle of the post-acetabular region (Fig. 7).

The excretory bladder (Fig. 7) is a contractile tube extending nearly to the ventral sucker, and ending posteriorly in a muscular-walled outlet duct leading to a terminal pore. The wall of the bladder is composed of very large cells 20 to 25 μ long and 10 to 15 μ wide, with spherical nuclei about 5 μ in diameter; these cells are filled with spherical granules or droplets as large as the nucleus. The excretory tubes, their branches, the capillaries, and the flame cells have the same arrangements as in the adult. The flame cell formula is $2[(2 + 2 + 2) + (2 + 2 + 2)]$; frequently all the capillaries and flame cells can be seen at one time in a single individual. In each pair of flame cells one cell is dorsal and the other ventral.

This cercaria is a very rapid and effective swimmer. In swimming the body is flexed ventrad, while the tail is extended to its maximum length and beats so rapidly that it may be seen only as a blurred area. Sometimes the tail leads and sometimes it pushes the body. There is a strong reaction to light: individuals which have just emerged from the host swim towards light, but after perhaps an hour they reverse this reaction and swim away from light. A swarm of cercariae may be driven from one side of a wide dish to the other in a few minutes by changing the direction of the light. When a swimming cercaria comes in contact with

a solid surface, the suckers secure a hold and progression by leech-like creeping begins. Usually the tail is cast off within a few minutes after creeping begins, and sometimes almost immediately.

METACERCARIA.—The metacercaria is found encysted in the muscles and body cavity of Hexagenia nymphs, usually in the gill-bearing segments of the abdomen. A few of the infested nymphs which emerged as sub-imagos in the laboratory were identified by Doctor Herbert Ross, of the Illinois Natural History Survey, as *Hexagenia limbata* (Guerin). However, it is possible that some of the hosts belonged to other species of Hexagenia. Of 191 Hexagenia nymphs collected in the Sangamon River between Mahomet and Fisher, Ill., from July 26, 1931, to July 17, 1932, *Crepidostomum cooperi* metacercariae were found in 141, or 74%. The greatest number of cysts found in a single naturally infested individual was 13; the average number of cysts in infested hosts varied from 1.9 to 6.7 in collections made at different times and places; the lowest percentage of infestation, 61%, was found in July and August, 1931, and the highest percentage, 95%, was found in July, 1932; no statement can be made as to the seasonal variation of infestation in this case, for the infestation remained between 61% and 95% during the winter. Apparently there is an increase in the number of metacercariae per host as one goes upstream.

The metacercaria is enclosed in a thin transparent true cyst about 0.19 mm. in diameter. Except in recent infestations, the true cyst is surrounded by a layer of orange-brown granular material laid down by the host, and this in turn is usually enclosed in a wall of closely packed connective tissue. The metacercaria lies doubled in a U-shaped position, almost completely filling the true cyst.

Living metacercariae removed from the cyst average about 0.30 mm. in length, ranging from 0.24 mm. contracted to 0.50 mm. extended, the width being about one-third of the length in the resting condition. The oral sucker averages 90 by 80 μ, the ventral sucker 60 by 70 μ; the ventral sucker is usually near the center of the body length. The oral papillae are exactly as in the adult except in absolute size. The prepharynx is short as in the adult, and the pharynx is the same size, in proportion to the suckers, as in the adult. The esophagus is several times as long as the pharynx, and the crura extend nearly to the posterior end of the body except in recently encysted individuals. The cephalic glands of the cercaria are present, but are smaller and more numerous (5 to 10 on each side) and stain brownish-red with neutral red; the ducts are as in the cercaria except for the increase in number. The stylet is present, in the same position as in the cercaria, in recently encysted metacercariae, but usually not in older ones. The eyespots are still conspicuous, and usually fairly compact. There are no cystogenous glands, even in meta-

cercariae which have just completed encystment; the true cyst takes the bright orange-red stain (with neutral red) which is characteristic of the cystogenous glands in the cercaria, so there can be little doubt that the secretions of these glands take part in the formation of the cyst. Long tubular cutaneous glands, most abundant in the anterior end and around the suckers, lie just under the surface of the body and open to the outside through pores scattered over the surface; the content of these glands is a homogenous, slightly light-refractive fluid which stains yellow in neutral red; the end of the ducts sometimes project as little papillae on the outside surface. The same glands can be seen in living adults; in sections they stain deeply with eosin and Orange G.

Recently encysted metacercariae differ from the cercaria only in the absence of the tail and of the cystogenous glands and in the altered staining reaction of the cephalic glands; in older specimens the genital organs become fully developed and differ from those of the adult only in their relatively larger size in relation to the size of the adult. In *C. cooperi*, unlike *C. cornutum*, the metacercaria does not become appreciably larger as long as it remains within the cyst. In old individuals the testes are very large and are producing numerous spermatozoa, the cirrus sac is relatively larger than in most adults and is much convoluted, the cirrus, pars prostatica, prostate glands, and seminal vesicle are fully developed, the vesicle is packed with active spermatozoa, and many spermatozoa can be seen in the uterus; the ovary and seminal receptacle are of about the same relative size as in the adult and their connecting ducts are fully developed, but the ovarian cells and vitellaria are still immature. It seems evident that such an individual would begin to produce eggs very soon after entering the adult host and would have to be considered an adult in spite of its minute size; such cases may account for the forms with unusually large testes and for the individuals with abnormally large cirrus sac which Van Cleave and Mueller have designated tentatively as "winter forms." So far I have never found a progenetic metacercaria, i.e., one which produces eggs while in the second intermediate host, although I have examined hundreds of metacercariae at all seasons of the year.

The excretory system of the metacercaria is exactly the same as in the cercaria, except that the excretory bladder is enormously swollen and filled with spherical light-refractive droplets, giving a dark steel-gray appearance when seen by transmitted light. The wall of the bladder is thin; one may surmise that the large cells which surround the bladder in the cercaria have discharged their contents into the bladder, thus giving rise to the peculiar droplets characteristic of the bladder in the metacercaria. The excretory droplets are forced out through the excretory

pore from time to time after a metacercaria begins to crawl around, and become less and less abundant after an individual enters the intestine of the host fish. The flame cells are of the same shape as in the cercaria and are little if any longer.

INFESTATION EXPERIMENTS.—A few attempts to infest young Musculium and Sphaerium by exposure to miracidia were made, but were unsuccessful.

Hexagenia nymphs were invariably infested successfully by exposing them overnight in syracuse dishes with a Musculium which was giving off cercariae. Attempts to study the process of penetration under the microscope were unsuccessful because of the sensitivity of the cercaria to light. Experimentally infested mayflies were examined alive under the microscope from time to time, and some were dissected at periods from 18 hours to 3 weeks after exposure; from 1 to 62 cysts were found on dissection. The metacercariae obtained in this way were identical with those found in naturally infested nymphs. After 24 hours, a newly encysted larva is still a cercaria to all appearances, except for the lack of a tail, and the host cyst is lacking. Within 4 days the orange-brown host cyst is formed and the excretory bladder has taken on the appearance characteristic of the metacercaria. Within 2 or 3 weeks the metacercariae are as fully developed as most of those found in natural infestations, and at this age they have been proved capable of developing into adults when fed to sunfish. The tail is never found in individuals which have penetrated into a mayfly, even in those which have not yet encysted.

A few attempts were made to infest Chironomus larvae, Sialis nymphs, dragon-fly larvae, crayfish, and Heptagenia nymphs, but without success. Cercariae penetrated into Chironomus nymphs in a few cases, but after crawling around in the body cavity for some time they all died without forming cysts. One cyst was obtained in the gill of a Heptagenia nymph, but the metacercaria died and degenerated within a few days. Cysts were occasionally obtained in the gills of Hexagenia nymphs after exposure to a heavy swarm of cercariae, but none were ever found in the gills of naturally infested hosts. No cysts were found in Heptagenia nymphs in nature, although nymphs of this genus were abundant in the Sangamon and 40 were examined. All mayfly nymphs used in infestation experiments were carefully examined under the microscope before exposure to cercariae, in order to avoid confusion with natural infestations.

Infested Hexagenia nymphs were fed to 11 sunfish, and adult or nearly mature *C. cooperi* were recovered from 8 of these. The species successfully infested were *Lepomis cyanellus, L. humilis,* and *L. megalotis.* These experiments showed that 3 to 4 weeks is the time required

by most individuals to develop into sexually mature adults after entrance into the fish host. *C. cooperi* was also obtained from 5 of 7 catfish (*Schilbeodes gyrinus, S. miurus,* and *Ameiurus melas*) which were fed infested nymphs.

The sunfish and 5 of the catfish used in these experiments came from the same Spoon River oxbow in which the cercaria of *C. cooperi* was found. These fish were kept in the laboratory from 1 to 4 months before feeding experiments were attempted. For controls I used 31 sunfish and 9 catfish from the same oxbow; of these, 6 sunfish and no catfish contained Crepidostomum. It may be worthwhile to note that no Hexagenia nymphs were ever found in this oxbow, although I searched for them many times. Probably there had been some Hexagenia here, but they had died out when the water became too stagnant.

Crepidostomum cornutum (Osborn 1903)

SYNONYMS.—*Bunodera cornuta* Osborn 1903; *Distomum nodulosum* Zeder of Wright 1884; *Distomum auritus* MacCallum 1918 (probably),

HOSTS AND LOCALITIES REPORTED.—

Centrarchidae: *Micropterus dolomicu,* Go-Home Bay, Flat Rock Lake, and Musquash River, Ontario; Douglas Lake, Michigan; Oneida Lake, *St. Lawrence River, and *Hatchery Pond at Ogdensburg, New York; *Middle Fork River at Penfield and *Pistakee Lake, Illinois. *Micropterus salmoides,* Money, Mississippi. "Black bass," Lake Chatauqua, New York. *Ambloplites rupestris,* Lake Chatauqua and Oneida Lake, New York; Montreal, Quebec (bought in market); Go-Home Bay, Ontario; *Put-in-Bay, Ohio; Lake Michigan, Wisconsin; St. Lawrence River. *Pomoxis annularis,* *Hetterson's Lake, Greene County, Alabama. *Lepomis* sp., Money, Mississippi. *Chaenobryttus gulosus,* Money, Mississippi.

Siluridae: "Catfish or bullhead," Lake Chatauqua, New York. "Channel cat," Lake Michigan, Wisconsin. "Yellow bullhead," Lake Michigan, Wisconsin. "Speckled bullhead," Lake Michigan, Wisconsin. *Ameiurus lacustris,* Flat Rock Lake and Musquash River, Ontario. "Catfish," *Baton Rouge, Louisiana. *Ameiurus melas,* Baton Rouge, Louisiana.

Amphibia: "Mud puppy," Lake Michigan, Wisconsin. *Amphiuma means,* Baton Rouge, Louisiana.

Invertebrates: *Cambarus* spp., Lake Chatauqua, New York; Alma, Michigan; Montreal (?), Quebec; Toronto (?), Ontario; Go Home, Killarney, and Shawanaga, Ontario; Minneapolis, Minnesota; *Madison, Wisconsin; Manhattan, Kansas; Baton Rouge, Louisiana; Mississippi (?); *Champaign County, Illinois.

C. cornutum was first described by Osborn (1903) as *Bunodera cornuta*. Stafford (1904) assigned Osborn's species to Crepidostomum. Since then numerous descriptions and reports by various investigators have made *C. cornutum* the best known American species of the genus, and have shown it to be abundant and widely distributed. The material used in my study of the adult includes Cooper's Ontario specimens and specimens collected by Hunter in New York, by H. J. Bennett in Louisiana, by myself in Illinois, by Dr. Ward at Put-in-Bay, by J. H. Walker in Alabama, by Simer in Mississippi, and by Cooper and by L. J. Thomas at Douglas Lake.

SPECIFIC DIAGNOSIS.—The following specific diagnosis of *C. cornutum* sums up all the knowledge now available:

With the characters of the genus. Length of sexually mature specimens 1.0 to 3.7 mm. long when fairly well extended; width usually about one-fourth to one-third of length, but may be less at maximum extension; greatest width usually at level of oral sucker, sometimes at ventral sucker. Oral sucker very large; ventral sucker one-half to three-fourths as large as oral sucker, in first or second fourth of body length. Length of ventral papillae about one-half diameter of oral sucker, four dorsal papillae only slightly smaller; none notched. Pharynx one-fifth to one-third as long as oral sucker. Esophagus two to four times as long as pharynx.

Common genital pore ventral or posterior to crural fork. Cirrus sac very long, slender, often curved or convoluted; always extending back past ventral sucker, often as far as anterior testis; posterior end bent ventrad. Seminal vesicle long, convoluted, occupying posterior half or two-thirds of cirrus sac; wall muscular; pars prostatica large; cirrus slender, straight or curved, with muscular wall of moderate thickness, and lumen lined with pointed projections. Testes ventral in posterior half of body, tandem to strongly oblique, highly variable in size and shape, sometimes contiguous and sometimes separated by a space equal to diameter of testis. Vasa efferentia from testes uniting just at posterior end of cirrus sac. Ovary relatively small, pear-shaped, dorsal, median or slightly lateral on either side, sometimes touching ventral sucker and sometimes behind it a distance equal to three times its own diameter. Laurer's canal opening on dorso-lateral surface above intestinal cecum of side opposite to seminal receptacle. Uterus running back from oötype to anterior edge of anterior testis, or exceptionally as far as center or posterior edge of posterior testis, then coiling anteriad; metraterm beginning near posterior edge of ventral sucker, only slightly more thick-walled than uterus, with very prominent blunt-pointed projections in its lumen. Intrauterine eggs operculate, thin-shelled, ellipsoidal, light yellow, with germ cell in single

cell stage; numbering one to 50 or exceptionally 100; size 65 to 90 μ by 35 to 68 μ in whole mounts, with average of 81 by 56 μ. Vitellaria lateral from pharynx to posterior end, follicles mostly dorsal, lateral, and ventral to esophagus and intestinal crura with few or none median to crura, occasionally meeting near ventral surface at posterior ends of crura; longitudinal vitelline ducts joined behind posterior testis; transverse ducts near middle of body length.

Excretory bladder broad, pouch-shaped, dorsal, extending forward to level of anterior testis or ovary. Flame cell formula $2[(2+2+2)+(2+2+2)]$.

Pigmented eyespots present, one on each side of pharynx, but becoming dispersed in older individuals. Cephalic glands of cercaria persisting in adult, numerous.

Redia and cercaria unknown. Metacercaria encysted in crayfish (*Cambarus* spp.), with eyespots and (in very recently encysted individuals) a stylet; becoming sexually mature and growing to full adult size while still encysted, and producing numerous eggs of normal appearance; cysts 0.26 to 2.0 mm. in diameter, metacercaria 0.32 to about 3 or 4 mm. long, exactly similar to adult in older individuals and differing only in proportions of body and development of genital organs in younger specimens; eyespots compact in smaller specimens; cephalic glands 6 on each side of body in young metacercariae, in 2 groups of 3 each, increasing to 8 or 10 on each side in older specimens; stylet of the same form as in *C. cooperi*, 22 μ long; excretory bladder a swollen sac reaching to anterior testis or ventral sucker and filled with refractive droplets, flame cell formula $2[(2+2+2)+(2+2+2)]$.

In Osborn's original description of *C. cornutum*, his Fig. 7 shows the uterus in one specimen running back behind the testes; Faust (1918) claims that this specimen must therefore be a "Bunoderan," but the other features shown are distinctly those of *C. cornutum*. Simer (1929) reports the uterus in some specimens of *C. cornutum* reaching well past the border of the anterior testis; I have studied the specimen from which his Fig. 4 was drawn, and found it to be *C. cooperi*, but in some specimens of *C. cornutum* in Simer's collection from Micropterus the uterus does extend back dorsal to the testes as far as the posterior edge of the posterior testis. Thus in both *C. cooperi* and *C. cornutum* the uterus in exceptional cases extends back to the posterior testis, showing in this respect a tendency toward the conditions normally found in Megalogonia and Bunodera; however, the uterus in Crepidostomum always remains a narrow tube instead of becoming a sac as in Bunodera. The uterus of *C. cornutum* differs from that of *C. cooperi* by the possession of numerous blunt-pointed projections into the lumen (very large in the metraterm) which stain heavily with hematoxylin.

I have used specimens from crayfish from Louisiana, Michigan, Wisconsin, Illinois, Minnesota, Kansas, and Ontario in my study of the metacercaria. The Kansas specimens are the ones reported but not identified by Scott (1915), and the Ontario material is part of Cooper's collection. All of Scott's specimens and some of Cooper's are sexually mature, containing up to 100 eggs in the uterus; I have also studied sexually mature specimens from Louisiana and Wisconsin crayfish. Numerous living metacercariae from Illinois and Louisiana crayfish were studied alive, so that I was able to work out the excretory system of the metacercaria, but no living egg-bearing specimens from crayfish could be obtained. The flame cell of the metacercaria has a vibratile organelle 10 to 12 μ long and 4 to 6 μ wide; the vibratile organelle of flame cells in immature specimens from *Micropterus dolomieu*, on which I worked out the excretory system of the adult, is 12 to 15 μ long and 4 to 6 μ wide.

The progenetic metacercariae, i.e., those which produce eggs, are exactly like the normal adult in size and structure, except that there seems to be a tendency for more eggs to be retained in the uterus and more spermatozoa to be retained in the seminal vesicle. The vesicle becomes enormously swollen in some cases so that the cirrus sac extends back past the level of the anterior testis and is wider than the ventral sucker. In many cases the space between the worm and its cyst is packed with hundreds of eggs, but the egg cell apparently does not begin the development of an embryo as long as the eggs remain within the cyst.

The presence of pigmented eyespots and a stylet in the young metacercaria indicates that the cercaria is of the ophthalmoxiphidiocercaria type.

Crepidostomum illinoiense Faust 1918

SYNONYM.—*Crepidostomum hiodontos* Hunter and Bangham 1932.

HOSTS AND LOCALITIES REPORTED.—*Pomoxis sparoides*, Illinois River at Havana, Illinois. *Hiodon tergisus*, Lake Pepin (Mississippi River), Wisconsin; Lake Erie. **Boleosoma nigrum*, *Go-Home Bay (Georgian Bay), Ontario.

Faust (1918) originally described this parasite from numerous specimens taken from a single crappie, *Pomoxis sparoides* (Lac.) at Havana, Illinois, by Dr. H. J. Van Cleave. The next report of the species was made by Pearse (1924), who found sixteen specimens in the intestine of a mooneye (*Hiodon tergisus*) caught in Lake Pepin, Wisconsin, which is merely a wide stretch of the Mississippi River. Pearse figured *C. illinoiense*, but gave no description. Pearse (1924a) repeated the same record without description or figure. Hunter and Bangham (1932) have described as a new species, *Crepidostomum hiodontos*, a distome represented by seventy-three specimens from *Hiodon tergisus* in Lake Erie.

The material I have used for the study of *Crepidostomum illinoiense* consists of a slide containing 12 toto mounts, including the specimens on which Faust's description was based, and whole mounts and serial sections made by me from specimens in the vial in Dr. Ward's collection from which Faust got his specimens. One specimen of this species in Dr. Ward's collection was collected by A. R. Cooper from *Boleosoma nigrum* at Go-Home Bay, Ontario. The type specimen of *C. hiodontos* (U.S.N.M. No. 8609) and Pearse's specimens of *C. illinoiense* (U.S.N.M. No. 7626) were used for comparison.

Study of Faust's original specimens (Fig. 16) makes it evident that the supposed differences betwen *C. illinoiense* and *C. hiodontos* are based on errors in Faust's description. The oral sucker is by no means "almost twice as large" as the oral sucker, as Faust states, but is very slightly if any larger, and in a few specimens the ventral sucker is the larger. The apparent length of the esophagus as seen in whole mounts does not exceed the length of the pharynx, due to convolutions lying nearly in the dorso-ventral plane, but in sections it can be clearly seen that the esophagus is much longer, in fact, up to three times as long as the pharynx. In *C. illinoiense,* or at least in all the specimens studied, the cirrus sac ends at the level of the ovary. The uterus in the more mature specimens is coiled back as far as the anterior edge of the anterior testis, and contains up to ten eggs in Faust's material.

Study of Hunter and Bangham's type specimen of *C. hiodontos* and of another specimen which was later sent me by Dr. Hunter reveals nothing which could be used to exclude them from *C. illinoiense*. The crura are wider than in Faust's specimens and the ventral sucker is slightly larger than the oral sucker, but these are evidently merely individual differences probably due to conditions at the time of fixation. Pearse's specimens show all intermediate conditions; some have wide crura, others have crura no wider than in Faust's material; some have an oral sucker larger than the ventral, others have the reverse relationship. It is evident that Pearse was correct in assigning his specimens to *C. illinoiense,* and that *C. hiodontos* Hunter and Bangham is a synonym of *C. illinoiense* Faust. It may be noted that in Hunter and Bangham's type specimen and in one of Pearse's specimens the uterus extends back as far as the center of the anterior testis. In one of Pearse's specimens the testes are distinctly oblique, not median tandem as is usually the case in this species.

SPECIFIC DIAGNOSIS.—An inclusive description of *C. illinoiense* may now be given as follows:

With the characters of the genus. Length of sexually mature specimens 0.45 to about 1.2 mm.; greatest width at ventral sucker or ovary,

averaging about one-fourth length. Suckers nearly equal; either oral or ventral sucker may be slightly larger than other (oral sucker averaging 0.10 by 0.09 mm., ventral sucker 0.08 by 0.10 mm. in Faust's specimens). Ventral pair of oral papillae usually curved dorsad or posteriad, length about one-half diameter of oral sucker; dorso-lateral pair slightly smaller; median dorsal pair smallest of all, length averaging about one-fourth diameter of oral sucker, shape rectangular, with a distinct vertical notch in the distal end. Pharynx ovoidal or ellipsoidal, but often directed ventrad so that it appears spherical in dorsal or ventral view, the true length being about half that of the oral sucker. Esophagus up to three times as long as pharynx, but usually looped in dorso-ventral plane so that it appears shorter. Crural fork a little in front of ventral sucker, near dorsal surface; intestinal crura running back nearly to posterior end of body, either equal or unequal in length.

Genital pore median, either ventral to crural fork or a little posterior to this level. Cirrus sac long and narrow, with thin but muscular wall, reaching back over ventral sucker to level of ovary, usually bent two or three times in its course; seminal vesicle convoluted, running through posterior two-thirds or three-fourths of sac; pars prostatica ovoid, of medium size; cirrus fairly thick-walled, either straight or slightly bent. Testes irregularly spherical or ellipsoidal, nearly equal, sometimes one or both elongated either transversely or longitudinally, close together in tandem position near ventral surface in anterior half or two-thirds of post-acetabular region. Ovary pear-shaped, dorsal, on either side of mid-line close behind ventral sucker; seminal receptacle pear-shaped, immediately behind ovary; Laurer's canal opening on dorsal surface just above intestinal cecum on side opposite to ovary (Figs. 17, 18); uterus running back to anterior edge of anterior testis and then forward over ventral sucker, becoming more convoluted with increase in age and maturity of individual; metraterm beginning at posterior edge of sucker, wall slightly thicker and more muscular than wall of uterus. Intra-uterine eggs ovoidal or ellipsoidal, 56 to 65 μ by 28 to 33 μ with average of about 61 by 30 μ; egg cell not segmenting within uterus. Vitellaria lateral and ventral to intestinal crura and extending from pharynx or from level about half-way between suckers nearly to posterior end of body, a few follicles also lying dorsal to crura and extending into inter-crural space between and anterior to testes; follicles filling up all available space behind testes, from one side to the other; a few follicles also lying dorsal and ventral to testes in some specimens.

Excretory bladder a narrow pouch near dorsal surface, extending forward as far as center of anterior testis; excretory pore terminal; excretory pattern and flame cell formula unknown.

Life history entirely unknown, but presence in adults of a pair of pigmented eyespots, usually somewhat dispersed, indicates that the cercaria possesses pigmented eyespots.

Crepidostomum isostomum Hopkins 1931

SYNONYMS.—None.

HOSTS AND LOCALITIES REPORTED.—*Aphredoderus sayanus,* East Lake Fork, Sadorus, Illinois.

Since my original description of this species (Hopkins 1931) no additional material has been obtained. It was found only in a small drainage ditch, which was subsequently dredged with the consequent destruction of the fish and Sphaeriidae; both fish and Sphaeriidae have come back to this stream since then, but there is now no Crepidostomum infestation. I have been able to learn a few more details of structure by further study of preserved material, which are added to the original description in the following specific diagnosis of *C. isostomum.*

SPECIFIC DIAGNOSIS.—With the characters of the genus. Length of sexually mature adults about 0.8 to 2.0 mm., width usually about one-fourth length, widest in region of testes. Suckers approximately equal, average diameter about one-ninth length of body, ventral sucker one-third to one-half body length from anterior end. Oral papillae large, length about one-third to one-half diameter of oral sucker; dorsal papillae equal, ventral pair usually slightly larger. Pharynx barrel-shaped or ellipsoidal, length usually about one-half diameter of oral sucker, esophagus two to four times as long as pharynx, crural fork dorsal to ventral sucker, crura running nearly to posterior end of body. Genital pore anterior to crural fork, usually about half-way between pharynx and ventral sucker. Cirrus sac very short and broad, ovoidal or sausage-shaped, length one to three times width, usually reaching back only to center of ventral sucker; wall thin and weakly muscled. Seminal vesicle much convoluted, longer than sac but because of coiling sometimes not occupying more than half of length of sac, while in others it reaches nearly to anterior end; pars prostatica large; cirrus thick-walled and heavily muscular. Testes large, variable in shape, usually slightly oblique. Ovary pear-shaped or nearly spherical, smaller than testes, dorsal, usually overlapping posterior margin of ventral sucker, usually slightly lateral on either side but sometimes median. Laurer's canal opening dorsal to intestinal cecum on side opposite to seminal receptacle. Uterus coiling back to anterior edge of anterior testis and then forward; metraterm with muscular wall nearly as thick as that of cirrus beginning dorsal to ventral sucker and opening into posterior side of minute genital atrium.

Intrauterine eggs few (up to about 20 in specimens studied), operculate, thin-shelled, 70 to 90 μ by 40 to 60 μ with average length about 83 μ; remaining in single-cell stage while in uterus. Vitellaria from level of genital pore to posterior end; follicles lateral to esophagus and intestinal crura, and also along median sides of crura behind testes, between testes, and between ovary and testes. Excretory bladder an undivided sac, usually expanded at anterior end, reaching to seminal receptacle; flame cell formula unknown, but at least 10 and probably more flame cells present on each side of body; flame cells like those of *C. cooperi,* vibratile cone 10 to 12 μ by 4 to 5 μ.

LIFE HISTORY.—The life history of *C. isostomum* is still not known with certainty. Rediae probably belonging to this species were found in 21 of 78 *Sphaerium notatum* Sterki from East Lake Fork in March and April, 1930, but cercariae were found in only 9 of these, the others containing only rediae with immature germ balls or daughter rediae. Only 16 Sphaerium were found in this stream in 1931, and none of these were infested.

The immature rediae found on the gills of *S. notatum* are exactly like the immature rediae of *C. cooperi* except for the pharynx, which is 40 to 67 μ long and 30 to 60 μ wide, averaging 50 by 45 μ. Mature rediae are 0.7 to 1.3 mm. long and 0.2 to 0.3 mm. wide; the pharynx is the same size as in immature rediae. As in *C. cooperi,* the gut of the immature rediae disappears at maturity; there are 6 unicellular glands around the gut, with ducts running into the prepharyngeal cavity, in immature rediae. The excretory system is similar to that of *C. cooperi;* as many as 18 flame cells have been counted in mature rediae.

The cercaria is an ophthalmoxiphidiocercaria very similar to that of *C. cooperi.* Nearly all of those found were too immature to show the complete structure, but the eyespots were always conspicuous. Three individuals were found which were not only fully mature but had apparently developed past the cercaria stage, for they showed the 6 oral papillae typical of the genus and a large pharynx drawn up close to the oral sucker, as in the metacercaria of other species of Crepidostomum (Fig. 14). A stylet was seen in several cercariae, but only one was measured; this was 31 μ long and of the same form as in *C. cooperi.* The atypical cercariae with oral papillae were 270 to 360 μ long and 100 to 110 μ wide, with tails 240 to 270 μ long, oral sucker 70 to 72 μ by 70 to 80 μ, ventral sucker 65 to 75 μ by 65 μ, pharynx 34 to 35 μ by 30 to 33 μ and compact pigment cup of the eyespot about 18 by 15 μ; the oral papillae are about 15 μ long. As will be seen from these measurements, the pharynx is about half as long as the oral sucker; this is significant in view of the fact that metacercariae of *C. cornutum* occur in crayfish

in the same stream, since the pharynx of *C. cornutum* is less than one-third as long as the oral sucker. There is apparently a high degree of probability that the rediae and cercariae found in *S. notatum* belong to *C. isostomum.*

Crepidostomum metacercariae probably belonging to *C. isostomum* were found in a few nymphs of *Hexagenia* sp. (erroneously called *Ephoron* sp. in my 1931 paper) collected in East Lake Fork. These metacercariae are very similar to those of *C. cooperi;* the principal point of difference is the position of the cirrus sac, which in these larvae reaches from near the pharynx to the anterior edge or center of the ventral sucker. No experiments could be made because of the scarcity of material, but the only evidence against their being *C. isostomum* is the fact that the oral sucker is somewhat larger than the ventral sucker in the metacercaria, while the suckers are practically equal in the adult; however, the great range in the relative dimensions of the two suckers in *C. cooperi* shows that this is not a serious obstacle to considering the metacercaria from East Lake Fork to be the larva of *C. isostomum.* Final determination must await the finding of more abundant material.

Crepidostomum auriculatum (Wedl 1857)

SYNONYMS.—*Distoma auriculatum* Wedl 1857; *Acrodactyla auriculata* (Wedl) Odhner 1910; *Acrolichanus auriculatus* (?) (Wedl 1856) Skworzoff 1927; *Acrolichanus similis* Wisniewski 1933.

HOSTS AND LOCALITIES REPORTED.—*Acipenser ruthenus* L., Danube River; Volga and Oka Rivers, Russia.

Since this species was originally described by Wedl, it has been discussed by several writers whose only knowledge of the form was obtained from Wedl's description, but nothing based on a study of actual specimens (except a brief mention of the excretory bladder and cirrus sac by Odhner 1910) was published until 1924, when Skrjabin reported two specimens from Russian sterlets. More recently Skworzoff (1927, 1928) has given a detailed description of *Crepidostomum auriculatum,* based on numerous specimens from sterlets (*Acipenser ruthenus*).

There is nothing to exclude this species from the genus Crepidostomum; it differs from other species in some respects, but there is no difference on which a clear-cut generic distinction can be founded, since the peculiar features of the species are merely slight modifications of. features found in other species of the genus or different in degree only. Lühe (1909) was correct in calling Wedl's species *Crepidostomum auriculatum.* Its nearest relative is *C. lintoni.*

SPECIFIC DIAGNOSIS.—A brief diagnosis of *C. auriculatum,* combining the data of Wedl and Skworzoff, may be stated as follows:

With the characters of the genus. Adults averaging 1.87 mm. in length, sometimes as long as 3 mm.; greatest width at or behind ventral sucker, equalling about one-fourth of length. Ventral pair of oral papillae overlapping ventral surface of oral sucker, larger than other two pairs, length equalling about one-third of diameter of sucker; median dorsal pair only about one-third as long as ventral pair; dorso-lateral pair smallest, length being about one-half that of median dorsal papillae. Oral sucker round (heart-shaped when flattened), diameter about one-seventh or one-eighth length of body, equal to ventral sucker or slightly larger; oral aperture usually triangular. Ventral sucker in anterior half of body, round in outline. Pharynx longer than broad; length about half that of oral sucker. Prepharynx short. Esophagus short, length averaging less than that of pharynx. Crural fork about one-third way from oral to ventral sucker, crura reaching past testes but not to posterior end of body.

Genital pore just behind crural fork. Cirrus sac very broad and long, in some cases reaching posteriorly beyond ventral sucker; length sometimes one-third body length; wall sparsely muscular. Seminal vesicle occupying more than half of cirrus sac, convoluted; pars prostatica present; cirrus thick-walled, strongly muscular, protrusible; prostate glands strongly developed and numerous. Ovary ovoidal, near dorsal surface on either right or left side close behind ventral sucker. Oviduct, seminal receptacle, Laurer's canal, oötype, and connections as in rest of genus. Uterus with few loops, not extending posteriorly beyond anterior testis. Eggs $64\,\mu$ by 36 to $38\,\mu$. Vitellaria along margins of body from pharynx to posterior end, meeting behind testes; transverse ducts near middle of body length, meeting to form vitelline reservoir. Excretory bladder long, sacculate-tubular, reaching anteriorly as far as ovary; main collecting tube on each side running from anterior end of bladder to level of ventral sucker, there dividing into anterior and posterior branches; flame cell formula unknown. Eyespots one on each side of pharynx. Cephalic glands numerous. Habitat, midgut of *Acipenser ruthenus*. Known distribution, rivers running into Black and Caspian Seas. Life history entirely unknown, but presence of eyespots in adults indicates that cercaria is eyespotted.

There were a few immature specimens of *C. auriculatum* in the material sent to Professor Ward from the University of Berlin Zoological Museum (Berlin No. 3247); they were collected by Collin from *Acipenser ruthenus*, locality unspecified. These are the only specimens I have had opportunity to examine, so I can add nothing to the knowledge of the species, except to say that the cephalic glands open dorsal to the oral sucker at the anterior end of the body as in other species, not into the oral cavity as Skworzoff states.

Recently Wisniewski (1933) has described a new species, *Acrolich-anus similis* Wisniewski 1933, from *Salmo fario* and *Salmo irideus* in the Bosna River near Sarajevo, Jugo-Slavia. As well as I can judge without seeing specimens of this form, *A. similis* is a synonym of *Crepid-ostomum auriculatum*. Wisniewski admits that the differences between his species and *C. auriculatum* as described by Skworzoff are slight and of secondary importance, relating only to the slightly different shape of the body, the form and position of the testes, and the absolute dimensions of the ovary and testes, but suggests that Skworzoff's form may be identical with *A. similis* and not with the true *C. auriculatum* of Wedl. He states that the ventral sucker of Skworzoff's form was described as being larger than the oral sucker, as in his own material; it is true that Skworzoff in one place gives the dimensions of the ventral sucker as slightly larger than the oral, but in another place he states that the oral sucker is slightly the larger, and the oral sucker is also shown larger in one of his figures. All the differences which Wisniewski claims to separate his species from Wedl's can easily be accounted for by the supposition that Wedl's specimens were extended and Wisniewski's somewhat more contracted and flattened under the cover slip, as his Fig. 1 seems to show.

Crepidostomum lintoni (Pratt in Linton 1901)

SYNONYMS.—*"Distomum auriculatum* Wedl (?)" of Linton 1898; *Bunodera lintoni* Pratt in Linton 1901; "Bunodera auriculata of Wedl 1857" of Osborn 1903; *"Crepidastomum auriculatum* (Wedl) Linton" of Pratt 1902; *Distomum petalosum* Lander in Looss 1902; *Acrodactyla petalosa* (Lander) Stafford 1904; *Acrodactyla lintoni* (Pratt) Odhner 1910; *Acrolichanus petalosa* (Lander) Ward 1917.

HOSTS AND LOCALITIES REPORTED.—*Acipenser fulvescens* (*A. rubicundus*), Great Lakes and St. Lawrence River. *Scaphirhynchus plator-hynchus*, Mississippi River (Lake Pepin), Wisconsin.

This species was first reported by Linton (1898) under the name of *"Distomum auriculatum* Wedl (?)," with a very brief description and vague figures. Later Linton (1901) again mentioned the species with only the comment "Pratt proposes the name *Bunodera lintoni* for this species." Pratt (1902) uses the name *"C. auriculatum* (Wedl) Linton" under the heading "Genus Crepidastomum," an obvious misprint. Looss. (1902) published the name *Distomum petalosum* C. H. Lander for specimens with this label sent to him by Lander, and stated that this species was to all appearances the same as that which Linton described as *"Distomum auriculatum* Wedl (?)" but was distinct from the true *D.*

auriculatum Wedl. Stiles and Hassall (1908) and Odhner (1910) therefore consider *D. petalosum* a synonym of *Bunodera lintoni,* the latter name having been published a year earlier. Ward (1917) considers Lander's species distinct from Linton's form. Stafford (1904) proposed the new genus Acrodactyla with *A. petalosa* (Lander) as type; this generic name was later found to be preoccupied, and Ward (1917) substituted the new name Acrolichanus for the genus. I cannot find any difference of more than specific value to separate Acrolichanus from Crepidostomum, and accordingly use the name *Crepidostomum lintoni* (Pratt in Linton 1901), considering *A. petalosa* a synonym. The only difference of any importance between Lander's and Linton's forms, so far as the present evidence goes, is the apparent difference in length and position of the cirrus sac, which is figured and described by Linton as being entirely in front of the ventral sucker, while in Lander's specimens it reaches at least as far back as the anterior edge of the sucker. This difference is probably not real, and in any case is overbalanced by the agreement in all other features and the specific identity of the hosts, both lots of specimens having been found in Great Lake sturgeons. Unfortunately Linton's specimens in the U. S. National Museum are no longer available for study, having become dried-up.
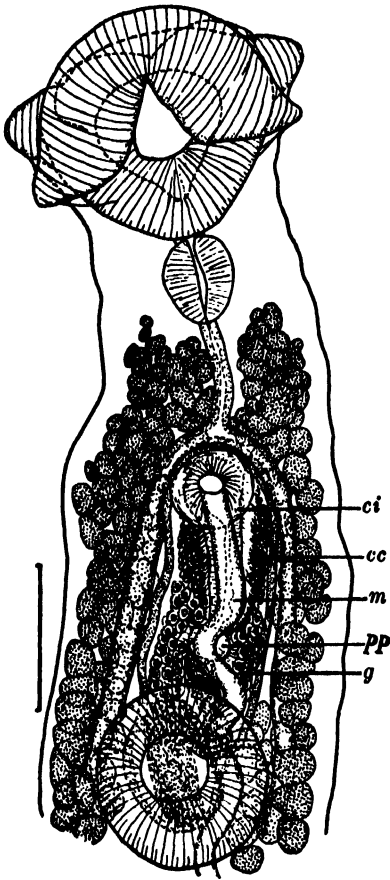
TEXT-FIG. 3.—Anterior end of *C. lintoni* adult; scale line represents 0.2 mm.; *cc,* cells connected with wall of cirrus; *ci,* cirrus; *g,* prostate glands; *m,* metraterm; *pp,* pars prostatica.

Although brief descriptions or notes based on study of actual specimens of *C. lintoni* have been published by Linton (1898), Looss (1902), Stafford (1904), Osborn (1903), Cooper (1915), Ward (1917), and Pearse (1924a), the only paper which

gives anything approaching a complete description is that of Faust (1918). However, Faust's inclusion of "specimens of Osborn's material from *Ambloplites rupestris*" is almost certainly erroneous.

The material used in my study of the species consists of two slides containing 5 whole mounts of Lander's original specimens from near Detroit, Michigan, numerous specimens collected by A. R. Cooper in the St. Lawrence River near Ogden Island and near Iroquois, Ontario, and Professor Ward's specimens collected in Lake St. Clair near New Baltimore, Michigan. All of these specimens are from the intestine of *Acipenser fulvescens*. They are now in the collection of Professor Henry B. Ward.

SPECIFIC DIAGNOSIS.—The following specific diagnosis is based on my study of the specimens in Professor Ward's collection, some of which were used also by Faust in his study:

Crepidostomum lintoni: With the characters of the genus. Length of sexually mature specimens from about 1.2 to about 3.0 mm.; width averaging a little less than one-fourth of length, greatest at level of anterior testis or at ventral sucker. Oral sucker about one-third larger than ventral sucker, diameter equal to about one-fifth to one-seventh of body length. Oral papillae nearly conical with somewhat rounded tips; ventral pair largest, overlapping ventral surface of oral sucker; dorso-lateral and median dorsal pair about equal. Ventral sucker near junction of first and second thirds of body length. Pharynx ovoidal, length one-third to one-half diameter of oral sucker. Esophagus muscular, length one to two times that of pharynx; crural fork only a short distance behind pharynx and usually far in front of ventral sucker.

Genital pore median just behind crural fork. Metraterm and cirrus joining just as they reach ventral surface. Cirrus sac broad, sausage-shaped, reaching back over ventral sucker as far as center or posterior edge; wall thick, muscular. Slender convoluted seminal vesicle, usually S-shaped in dorsal view, occupying posterior half of sac; pars prostatica large, ovoidal; cirrus very strongly muscular, thick-walled, often giving the appearance in whole mounts of a genital sphincter (which does not exist); prostate glands large, numerous, filling most of the space in middle third of sac (Text-fig. 3). Testes in posterior half or posterior third of body, tandem or oblique, close together, round or slightly lobate; vasa efferentia joining after entering cirrus sac. Ovary pear-shaped, margins entire or slightly lobed, dorsal just behind ventral sucker, median or slightly lateral on either side. Oviduct, seminal receptacle, vitelline reservoir, oötype and connections as in rest of genus; Laurer's canal opening on dorsal surface only slightly to one side of median line.

Uterus running back in more or less convoluted course ventral and lateral to anterior testis, turning anteriad near anterior edge or center of posterior testis and then running forward; metraterm beginning near center of ventral sucker, with fairly thick muscular wall. Intrauterine eggs one to 30 (in specimens studied to date), ovoidal or ellipsoidal, 50 to 72 μ by 25 to 40 μ with average about 61 by 33 μ; egg cell remaining in single-cell stage until egg is laid. Vitelline follicles along margins of body from pharynx nearly to posterior end, surrounding crura on dorsal, lateral, and ventral sides and overlapping the testes to a slight extent dorsally and ventrally, but never extending inward to median line except behind testes, where they may or may not meet in median line near dorsal surface. Transverse vitelline ducts meeting to form vitelline reservoir immediately behind ovary.

Excretory bladder a long pouch lying near dorsal surface, extending anteriorly as far as seminal receptacle or ovary. Main collecting vessels running forward from each side of anterior end of bladder and dividing lateral to posterior edge of ventral sucker into an anterior and a posterior branch. Flame cell formula unknown.

Life cycle unknown; the metacercariae have been reported from cysts in crayfish (*Cambarus* sp.) but these were probably *C. cornutum*. Remnants of eyespots in immature specimens from sturgeons prove that cercaria and metacercaria must have eyespots. Cephalic glands also present in adults, opening dorsal to anterior edge of oral sucker.

Faust (1918), using Lander's unpublished notes and drawings, now in the possession of Professor Ward, says that as many as 6 flame cells have been found anterior to the forking of the excretory system and 8 have been found posterior to the forking. Later Faust (1919) gave the flame cell formula $12 = (2 + 2) + (2 + 2 + 2 + 2)$ for the "larva," and later still (1924) lists the formula $2[(2 + 2) + (2 + 2 + 2 + 2)]$ for the adult. This formula is obviously inconsistent with the statements made in the 1919 paper; in a letter to me, dated Sept. 29, 1932, Faust admits this inconsistency and states that he does not now know the source of his later formula. Lander's original drawings of his crayfish specimens clearly show them to be metacercariae of *C. cornutum*. Lander's drawing of the excretory system was made from the crayfish form, not from adults; so the formula given by Faust has nothing to do with *C. lintoni*.

Faust (1919) very briefly describes and figures, from drawings made by Professor Ward, a metacercaria found by Ward in *Cambarus* sp. at Ann Arbor, Michigan. According to Faust, this is the "larva" of *C. lintoni*, but it might equally well belong to *C. cornutum*, and since no evidence is presented which would distinguish it from the latter species, its status must still be considered doubtful.

Crepidostomum canadense Hopkins 1931

SYNONYMS.—None.

HOSTS AND LOCALITIES REPORTED. — *Boleosoma nigrum,* Go-Home Bay, Ontario.

I have nothing more to add to my original description of this species (Hopkins 1931a). While the species appears to be distinct on the basis of the meager material at hand, it is possible that the finding of more abundant and better preserved specimens may show that *C. canadense* is identical with *C. isostomum,* with which it is undoubtedly closely related.

Crepidostomum latum (Pigulewsky 1931)

SYNONYM.—*Stephanophiala lata* Pigulewsky 1931.

HOSTS AND LOCALITIES REPORTED. — *Scardinius erythrophthalmus* (L.), Ukraine, U.S.S.R.

This species is known only from two specimens from the intestine of *S. erythrophthalmus.* According to Pigulewsky's brief description, the anterior end is tapered, the body being broadest in the region of the ventral sucker. The cuticula is without spines. The length is 1.03 to 1.3 mm., the breadth 0.191 to 0.195 mm. The pharynx is 65 μ long, 43 to 54 μ wide. The oral sucker is 0.143 to 0.165 mm. long, 0.056 mm. wide. The two intestinal crura are separate and do not reach the posterior end of the body. The vitelline follicles are 52 μ in diameter, and do not extend anteriorly as far as the ventral sucker. The ovary is ovoidal, 0.147 mm. long and 0.130 to 0.143 mm. wide. The uterus lies between the ventral sucker and the anterior testis. The eggs are without filament, and are 87 to 91 μ long, 43 to 56 μ wide. The testes are ovoidal; the anterior testis is 0.247 to 0.260 mm. long and 0.174 mm. wide, the posterior 0.221 to 0.260 mm. long and 0.147 to 0.174 mm. wide. The cirrus sac is sack-shaped, bent in the form of the letter S, and does not reach anteriorly past the level of the crural fork or posteriorly to the posterior edge of the ventral sucker; it is 0.108 to 0.152 mm. long. The seminal receptacle is 0.087 by 0.108 to 0.130 mm.

Pigulewsky's single figure, evidently drawn from a strongly contracted specimen, shows a distome resembling *C. farionis* in general appearance, but differing from this species in the position of the genital pore behind the crural fork, (this is not definitely shown, however), the restriction of the vitellaria to the post-acetabular region, and the positions of the ovary and seminal receptacle. The receptacle is shown dorsal and posterior to the ventral sucker in the median line, while the ovary is lateral and posterior to the receptacle. Twenty-three eggs are shown in the uterus. No esophagus is shown, but presumably the esophagus is present, though

looped in the dorso-ventral plane as in other species when the body is strongly contracted. If Pigulewsky's description and figure are correct, *C. latum* is distinctly set off from all other known species of Crepidostomum by the restriction of the vitellaria to the post-acetabular region, although its resemblance to *C. farionis* in most features is very striking.

<h3 align="center">Genus Megalogonia Surber 1928</h3>

Since the publication of Surber's (1928) description of the genus, the type and only species, *Megalogonia ictaluri,* has been restudied by Walz (1933) and by myself. These studies have shown that Surber's description of *M. ictaluri* is at fault in several instances. I give below a definition of the genus Megalogonia based on the present knowledge of the type species:

Allocreadiidae with six muscular oral papillae consisting of four dorsal and two ventral outgrowths from the oral sucker; two testes in tandem arrangement each divided by a median longitudinal constriction into a right and left lobe; uterus extending back between the lobes of the testes, sometimes to the posterior end of the body, sometimes only to the center of the anterior testis, then running forward in nearly the same course; intrauterine ova large and comparatively few as in Crepidostomum, not undergoing segmentation while in uterus; seminal receptacle, Laurer's canal, Mehlis glands, vitelline reservoir present and arranged as in Crepidostomum; genital pore median, ventral, in front of ventral sucker; cirrus sac containing seminal vesicle, pars prostatica, cirrus, and prostate glands, the long muscular cirrus taking up over half the length of the cirrus sac; excretory bladder sacculate, extending only to anterior end of posterior testis or to posterior end of anterior testis, with a collecting tube running forward from its anterior end on each side of the body and dividing near the ventral sucker into an anterior and a posterior branch which run along the margins of the body to the two ends, each of these primary branches dividing to give the flame cell formula $2[(2 + 2 + 2) + (2 + 2 + 2)]$; an eyespot on each side of the pharynx or esophagus except in older individuals. Miracidium developing within eggshell in water after laying, furnished with two fused pigmented concave eyespots, a rudimentary gut, two flame cells, and a coat of long cilia covering the body; no cuticular plates. Rediae long, slender, with large pharynx and rudimentary gut, no ambulatory processes; developing in Sphaeriidae; giving rise to more rediae or to cercariae. Cercaria a minute ophthalmoxiphidiocercaria with slender tail. Metacercaria encysted in aquatic insect larvae. Adult in intestine of fresh-water fishes. Type and only known species, *M. ictaluri.*

Megalogonia ictaluri Surber 1928

SYNONYMS.—None.

HOSTS AND LOCALITIES REPORTED.—*Ictalurus punctatus,* St. Croix River and Mississippi River, Minnesota; Rock River, Illinois. **Schilbe-odes gyrinus,* *Spoon River at St. Joseph, Ill. **Schilbeodes miurus,* Spoon River at St. Joseph, Ill.

The material I have used in the study of the adults of *M. ictaluri* consists of about 60 specimens from *Schilbeodes gyrinus* and *S. miurus,* of which 6 were obtained from a natural infestation and the rest from experimentally fed catfish, and 20 specimens from *Ictalurus puncta-tus* collected by Walz at the mouth of Rock River and used in his study (Walz 1933). Living specimens were studied thoroughly; the details of the reproductive system were worked out in living specimens and checked by the study of serial sections, and the excretory system was worked out in living adults in which the vitellaria had not yet developed enough to obscure the capillaries and flame cells. Surber's type specimen, U.S.N.M. No. 7966, and two paratypes, U.S.N.M. No. 7967, were studied and com-pared with my material.

There are three major errors in Surber's description: 1. In addition to the two ventral papillae which Surber saw there are four dorsal papil-lae, which can be seen on Surber's type specimen, and the six papillae are arranged as in Crepidostomum and Bunodera. 2. Laurer's canal is not absent, but present and complete, opening on the dorsal surface; this is distinctly visible in the type specimen. 3. The testes are not four sepa-rate organs; there are really only two testes, each divided by a median longitudinal constriction into two lateral lobes, more or less completely separated in some specimens and broadly joined in others.

SPECIFIC DIAGNOSIS.—A specific diagnosis of *Megalogonia ictaluri* based on my study is given below:

With the characters of the genus. Pyriform to elongate. Length of mature specimens 0.6 to 1.5 mm.; width about one-fourth of length, greatest in region between ventral sucker and posterior testis. Ventral sucker usually slightly larger than oral sucker, from anterior third to middle of body. Two ventral oral papillae projecting laterad from sides of oral sucker, four blunt dorsal papillae in line across dorsal surface of sucker and projecting dorsad; all six about equal. Prepharynx short; pharynx ovoidal or ellipsoidal, one-third to one-half as long as oral sucker. Esophagus thick-walled, two or three times as long as pharynx, usually convoluted; posterior end dividing just before running into in-testinal crura. Crural fork some distance in front of ventral sucker, crura running back dorsally near lateral margins and ending about half-

way between posterior testis and posterior end of body. Genital pore
median just behind crural fork. Cirrus sac with thin but muscular wall,
very long and slender, either straight or bent, reaching back over ventral
sucker to level of ovary; seminal vesicle usually convoluted, occupying
posterior one-third or two-fifths of sac, anterior end narrowing to slender
duct leading to small ovoidal or ellipsoidal pars prostatica near middle of
sac; slender cirrus with strongly muscular but not very thick wall running
from pars prostatica to genital pore; prostate glands comparatively few
and small, lying in middle third of sac. Testes two, very large, filling
nearly all intercrural space posterior to seminal receptacle; contiguous,
tandem, near ventral surface; usually each divided by median longitudinal
constriction into right and left lobe with only a narrow connection, but
connection varying from small duct to broad bridge nearly as wide as
lobes (Fig. 19, Text-fig. 4) ; margins of lobes usually somewhat notched
or lobate but sometimes smooth; vasa efferentia from each testis joining
just at posterior end of cirrus sac to form very short vas deferens which
immediately enters the sac and joins the seminal vesicle. Ovary dorsal
on either side of median line close behind ventral sucker, pear-shaped
(Fig. 15, Text-fig. 4). Seminal receptacle large, pear-shaped, dorsal,
immediately behind ovary. Laurer's canal opening on dorsal surface a
little median to intestinal cecum opposite to seminal receptacle. Oviduct,
oötype, shell glands and connections as in *Crepidostomum cooperi* (see
p. 9). Uterus increasing in length and convolutions with age, reaching
only to anterior edge of anterior testis in young adults, but in old indi-
viduals running back between lateral lobes of testes, on dorsal side,
nearly to posterior end of body before turning ventrad and running an-
teriad; wall of uterus thicker than in Crepidostomum, lumen lined with
protoplasmic projections; metraterm with thicker and more muscular
wall beginning at posterior edge of ventral sucker. Intrauterine eggs one
to 20 or more, operculate, about 61 by 38 μ in mounted specimens and
65 to 75 μ by 43 to 50 μ when free in water before fixation; remaining
in single cell stage while in uterus. Vitellaria from posterior end of oral
sucker nearly to posterior end of body; follicles from midline of dorsal
surface nearly to margins of body in pre-acetabular region, dorsal and
lateral to esophagus and crura; lateral and ventral to crura from ventral
sucker to behind testes, with a few follicles median to crura between and
in front of testes; extending completely across ventral surface behind
testes; longitudinal vitelline ducts of two sides uniting ventral to excre-
tory bladder behind testes; transverse vitelline ducts meeting to form
vitelline reservoir of variable size and form ventral or posterior to sem-
inal reservoir.

Excretory bladder narrow, sacculate or tubular, undivided, close to dorsal surface, ending between center of posterior testis and center of anterior testis. Collecting tube running forward from each side of an-
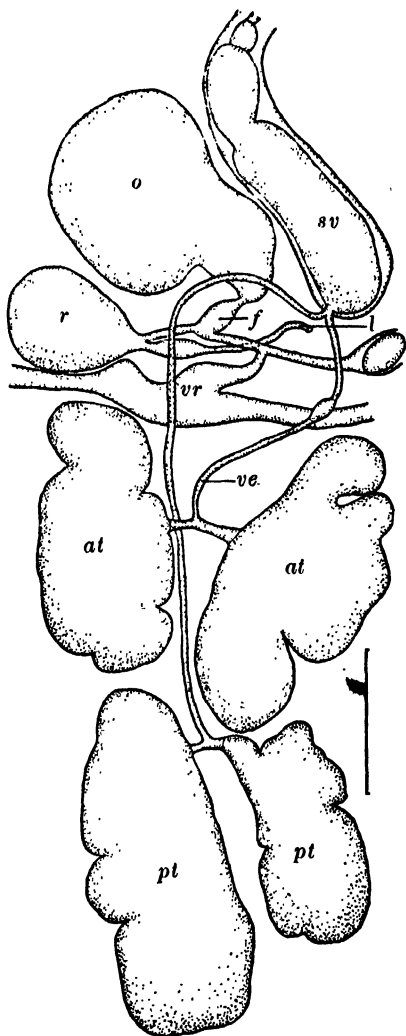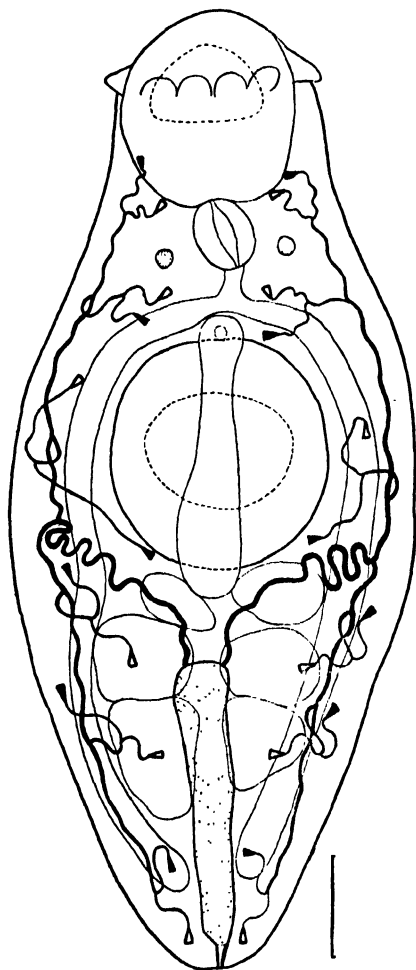
(4)   (5)

TEXT-FIG. 4.—Reproductive system of *M. ictaluri*, drawn from living specimen, ventral view; scale line represents 0.2 mm.; *at*, anterior testes; *f*, fertilization chamber; *l*, Laurer's canal; *o*, ovary; *pt*, posterior testes; *r*, seminal receptacle; *sv*, seminal vesicle; *ve*, vas efferens; *vr*, vitelline reservoir.

TEXT-FIG. 5.—Excretory system of *M. ictaluri*.

terior end of bladder, dividing lateral to posterior edge of ventral sucker into an anterior and a posterior branch; flame cell formula $2[(2+2+2)+(2+2+2)]$, one flame cell of each pair dorsal and one ventral; vibratile organelle of flame cell 15 by 8 μ in mature adults, conical.

Miracidium completely ciliated, without cuticular plates, with two fused pigmented eyespots and one pair of flame cells. Rediae in *Musculium transversum,* elongate sausage-shaped, with pharynx 40 to 52 μ by 30 to 45 μ. Cercaria of ophthalmoxiphidiocercaria type, about 200 to 250 μ long, with slender tail slightly shorter than body, stylet 15 μ long. Metacercaria encysted in gills of mayfly nymphs of genus Hexagenia, not increasing in size to any significant extent and not becoming sexually mature while in cyst. Metacercaria and young adults retaining pigment of eyespots. Adults in intestine of Siluridae.

MIRACIDIUM.—Cleavage of the germ cell begins as soon as the egg is laid; a well-developed miracidium is formed within 6 days, and hatching occurs in 8 or 10 days after the egg is laid. Because of its power of extention and contraction the miracidium is variable in shape; it may be pear-shaped or ovoidal when contracted and elongate-ellipsoidal when extended, the length varying from 45 to 85 μ and the width from 30 to 40 (Figs. 20, 21). The long cilia, arranged in numerous longitudinal rows very close together, cover the entire body without a break, and there are no cuticular plates. A rudimentary pear-shaped gut, extending back only one-third or one-fourth of the body length, opens at the tip of a conical inversible papilla at the anterior tip of the body. A pair of concave pigment cups surrounding the eyespots lie dorsal to the gut, fused together on their median convex sides. A pair of large flame cells lie in the equator of the body. The posterior half of the body contains germ cells. The pigment cups of the eyespots are about 10 μ in diameter and the organelles of the flame cells are 6 to 8 μ by 3 to 4 μ.

REDIA AND CERCARIA.—The redia and cercaria were found only once, in a *Musculium transversum* collected July 17 in the Sangamon River near Fisher, Illinois. Most of the cercariae were immature and the host died soon after being brought into the laboratory, so no adequate study could be made. The rediae are of the same type as those of *Crepidostomum cooperi,* but the mature ones are more slender; the pharynx is about 40 to 52 μ by 30 to 45 μ. The smallest immature redia measured was 200 μ long and 60 μ wide; the smallest redia containing well developed cercariae was about 0.5 mm. long and the largest was about 1.2 mm. long and 0.11 mm. wide.

The cercaria is about 200 to 250 μ long, with a slender tail somewhat shorter than the body. Identification was made by means of the stylet, which is of the same shape as that of *C. cooperi* but only 15 μ long, i.e.,

only about two-thirds as large as in *C. cooperi,* and is identical with the stylet found in the metacercariae of *M. ictaluri* (Fig. 8). Two dark pigmented eyespots lie laterally a short distance behind the oral sucker. Further than this nothing is known, as most of the cercariae were either dead or immature when studied.

METACERCARIA.—The metacercaria occurs in cysts in the gills of *Hexagenia limbata* Guerin and probably also in other species of Hexagenia; a few cysts have been found in the lateral margins of the abdomen, but not in the body cavity. From July 26, 1931, to July 17, 1932, I examined 191 Hexagenia nymphs from the Sangamon River between Mahomet and Fisher, Illinois, and found Megalogonia cysts in 91, or 48%. The highest degree of infestation, 80%, was found in the autumn and the lowest, 15%, in the spring months. The number of cysts in naturally infested hosts ranged from 1 to 40 with an average of 4.6 per host individual.

The living metacercaria when released from the cyst is about 0.25 mm. in the resting position, 0.40 mm. when extended and 0.15 mm. when contracted, the width varying from 0.09 to 0.15 mm. The two suckers are practically equal in recently encysted individuals but the ventral sucker becomes distinctly larger than the oral in older individuals, in which the average dimensions are 47 by 54 μ for the oral sucker and 62 by 67 μ for the ventral sucker. The six oral papillae are very small, but have the same structure and arrangement as in the adult (Text-fig. 6). The digestive system is exactly the same as in the adult except in very recently encysted metacercariae, in which the crura reach only about half way from ventral sucker to posterior end. The stylet is present in the younger metacercariae; its location and shape are as in *Crepidostomum cooperi,* but it is only about 15 μ long (Fig. 8). The eyespots, one on each side of the pharynx or esophagus, are compact in most specimens; each pigment cup is about 10 μ in diameter. There are 3 to 6 cephalic glands on each side of the esophagus or crural fork; they are pear-shaped, 20 to 30 μ long and 10 to 15 μ wide;
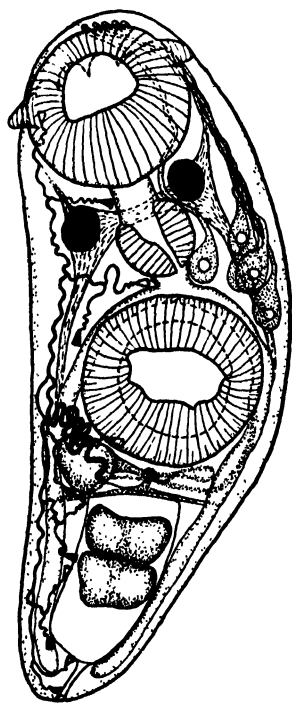
TEXT-FIG. 6.—Metacercaria of *M. ictaluri,* drawn from living specimens, ventral view.

the cytoplasmic contents are granular and stain red with neutral red in the living animal; the ducts run forward in two tracts on each side of the body and open through pores on the dorsal surface over the anterior margin of the oral sucker (Text-fig. 6). The excretory system is as in the adult except for the great distension of the excretory bladder, which fills most of the postacetabular region; the bladder is filled with excretory droplets as in Crepidostomum; the flame cells are of the same shape as in the cercaria and metacercaria of *C. cooperi*, but are smaller. The reproductive system is represented only by anlage in the younger metacercariae, but in older specimens all the organs and their ducts are present in the same arrangement as in the adult, except that the cirrus sac and uterus are shorter. There is the same variation in the shape of the testes in the metacercaria as in the adult (Text-fig. 6; Fig. 23 on Pl. IV).

Hexagenia nymphs containing Megalogonia metacercariae were fed to 7 catfish (*Schilbeodes gyrinus, S. miurus,* and *Ameiurus melas*) and 5 of these yielded Megalogonia when dissected. Sexually mature adults were found 14 to 16 days after the feeding. Two of the experimental fish were from the Salt Fork River near St. Joseph and the others were from the same oxbow of the Spoon River in which I found most of my *C. cooperi* cercariae. Two *A. melas* from this oxbow gave negative results after experimental feeding. All of the experimental fish were kept in the laboratory several weeks before feeding experiments were started. Megalogonia was found in only 1 of 9 control catfish which were caught · in the same Spoon River oxbow and dissected immediately. Attempts to infest a *Pomoxis sparoides* and several *Lepomis* spp. were unsuccessful.

GENUS BUNODERA Railliet 1896

Until recently *B. luciopercae,* the type of the genus, has been the only species of Bunodera known, but the finding of *B. sacculata* Van Cleave and Mueller, and restudy of *B. luciopercae,* make it necessary to revise the previous conception of the genus. The present knowledge of the genus Bunodera is summarized in the diagnosis given below.

Aberrant Allocreadiidae with six muscular oral papillae projecting from the oral sucker, of which two are ventral and four dorsal. Suckers large and approximately equal. Prepharynx, pharynx, and long muscular esophagus present, the esophagus (in some at least) dividing before running into the intestinal crura; crural fork some distance anterior to ventral sucker except in strongly contracted specimens; crura running nearly to posterior end of body in some, ending . in third quarter of body in others, close to dorsal surface in all. Genital pore ventral and median or slightly lateral, between suckers and anterior, ventral, or posterior to

crural fork. Cirrus sac broad and short, with thin but muscular wall; sac containing large seminal vesicle, pars prostatica, strongly muscular cirrus, and prostate glands; anterior end of sac eversible. Testes two, near ventral surface behind ovary in strongly oblique position; both close behind ovary in some, posterior testis in hind end of body in others. Vasa efferentia from testes running forward and entering vesicle separately. Ovary pear-shaped, near dorsal surface behind ventral sucker, median or lateral to median line on either right or left side. Seminal receptacle present (at least in *B. luciopercae*) near dorsal surface close behind ovary; pear-shaped, increasing in size with age. Oviduct leaving median side of ovary, soon widening to fertilization chamber, receiving seminal duct from receptacle at distal end of fertilization chamber, then running ventrad to oötype; common vitelline duct opening into oviduct between seminal duct and oötype; lumen of oviduct ciliated throughout. Laurer's canal coming off of seminal duct near seminal receptacle, running to pore on dorsal surface to one side of median line (dorsal to intestinal cecum on opposite side from ovary in *B. luciopercae*). Shell glands surrounding and opening into oviduct and oötype. Uterus running back from oötype to or nearly to posterior end of body, then turning anteriad and widening to broad pouch filling almost entire width and depth of body, narrowing again to narrow tube near posterior edge of ventral sucker; metraterm, with thick muscular wall, beginning dorsal to ventral sucker and running to genital sinus when this is present. Intrauterine eggs one to 5000 or more, ellipsoidal, 60 to 100 μ long; shell thin, yellowish, operculate; miracidium sometimes developing within intrauterine eggs. Vitellaria from pharynx to level of posterior testis or to posterior end of body, mostly lateral to intestinal crura, extending into intercrural space posterior to testes in some (*B. luciopercae*) and anterior to ovary in others (*B. sacculata*). Longitudinal vitelline ducts joined behind testes; transverse ducts meeting posterior or ventral to ovary to form vitelline reservoir, from which common vitelline duct runs to oviduct. Excretory bladder a broad dorsal sac, reaching to level of seminal receptacle or ovary; collecting tube running from each side of anterior end of bladder to level of ventral sucker, there dividing into anterior and posterior branch, each of which gives rise eventually to three groups of flame cells; excretory pattern same as that of Crepidostomum except that there are three or four flame cells in each group. Miracidium entirely ciliated, with pigmented eyespot in form of two fused cups, one pair of flame cells, no cuticular plates. Redia, cercaria and metacercaria not known, but adult has a pair of eyespots and cercaria must also have eyespots. Adults in intestine and pyloric ceca of fresh-water fishes. Type species, *B. luciopercae.* (Müller 1776)

Bunodera luciopercae (O. F. Müller 1776)

SYNONYMS.—*Fasciola lucio-percae* O. F. Müller 1776 (p. 223); *Fasciola percae cernuae* O. F. Müller 1776 (p. 224); *Planaria lagena* Braun 1788; *Fasciola percae* Gmelin 1790; *Fasciola percina* Schrank 1790; *Fasciola nodulosa* Froelich 1791; *Distoma nodulosum* Zeder 1800; *Crossodera nodulosa* Cobbold 1860; *Bunodera nodulosa* Looss 1899.

HOSTS AND LOCALITIES REPORTED.—*Lucioperca sandra*, Denmark; Germany. *Acerina cernua*, Denmark; Germany; Saratow, Russia. *Perca fluviatilis*, Germany; Sweden; France. *Aspro vulgaris*, Europe (fidé Schrank 1790). *Aspro zingel*, Europe (fidé Schrank 1790). *Esox lucius*, Europe (fidé Dujardin 1845). *Barbus barbus*, Germany. *Barbus fluviatilis*, France (fidé Dujardin 1845; Looss 1894 says not *B. luciopercae*). *Salmo trutta*, England; Scotland. *Perca flavescens*, Canada; United States.

The most complete description of *Bunodera luciopercae* is that given by Looss (1894), who studied both living and sectioned specimens. I have examined European specimens from the University of Berlin Zoological Museum (Vial No. 1568) and from the Königsberg Museum, and have found them to agree with Looss's description in every point except the following: (1) The excretory bladder is not forked, and does not end behind the testes as shown in his figures; instead, the bladder is a broad undivided sac, extending forward near the dorsal surface as far as the seminal receptacle. (2) The vitellaria are not dorsal to the level of the uterus, but lateral to the uterus and lateral and ventral to the intestinal crura (Figs. 22, 24, 25); they sometimes end before reaching the posterior tip of the body, as described and figured by Looss, but in most specimens the follicles extend to the posterior tip and meet behind the posterior testis, in the median line. (3) The eggs are not "nearly 100 μ long and about 50 μ wide," but only 66 to 70 μ by 43 to 51 μ in the Berlin material and 70 to 75 μ by 45 to 50 μ in the Königsberg specimens. It is possible that Looss made his measurements from living material, which would account for part but not all of this difference in egg size. The Berlin specimens were from the collection of Rudolphi.

I have also studied American specimens of *B. luciopercae* from the intestine of *Perca flavescens*, collected by Dr. A. R. Cahn from Lake Oconomowoc, Wisconsin (in January and August, 1923), and by Mr. M. A. Kemper from Lake Michigan (in April, 1913). Both of these collectors deposited numerous specimens in the collection of Professor Ward, and I have studied them both in toto and in sections. This is probably the same species that Stafford (1904) has reported from perch bought in the Montreal market and that Pearse (1924) has found abundant in the perch of Wisconsin lakes.

The American specimens which I have studied are all sexually mature (i.e., the uterus contains eggs of normal size and shape), and range from 1.0 to 3.6 mm. in length. The 1 mm. specimens are much contracted, and would probably measure about 1.5 mm. if even moderately extended. The width varies from one-fifth of the length in well-extended specimens to one-half of the length in much contracted individuals. The body is nearly round in cross-section (Fig. 22); the widest and deepest part of the body is usually about half-way between the ventral sucker and the posterior end; in well-extended individuals the pre-acetabular region is narrow and neck-like (Fig. 29), but in contracted specimens it is almost as wide as the post-acetabular region. The American specimens agree perfectly with those from Berlin and Königsberg except for the larger size of some of the American specimens, all of which however are well within the range of size given by Looss and others for European specimens. The eggs in the American material are 63 to 82 μ long and 38 to 51 μ wide, with an average of 71 by 43 μ; segmentation of the germ cell and formation of a partially developed embryo occurs within the intrauterine eggs, but so far I have not seen any which have developed to the miracidium stage.

SPECIFIC DIAGNOSIS.—The following specific diagnosis of *Bunodera luciopercae* applies to both European and American specimens:

Bunodera luciopercae (O. F. Müller 1776). With the characters of the genus. Length of mature adults 1.0 to 4.5 mm., width one-fifth to one-half length; body round in cross-section, usually widest in middle of post-acetabular region. Suckers nearly equal, diameter one-eleventh to one-fifth length of body; ventral sucker in anterior third or half of body. Dorsal papillae slightly larger than ventral pair; length of dorsal papillae one-fifth to one-third diameter of oral sucker, length of ventral papillae one-seventh to one-fourth. Prepharynx short. Pharynx ellipsoidal, averaging two-fifths length of oral sucker with extreme range of one-third to one-half. Esophagus two or three times as long as pharynx, convoluted in contracted specimens; posterior end dividing just before running into crura. Intestinal crura running from crural fork, a short distance anterior to ventral sucker, back nearly to posterior tip of body; close to dorsal surface and lateral margins of body throughout.

Common genital pore median or slightly to one side of median line, ventral to crural fork or very slightly in front or behind this level. Male and female ducts joining almost at common pore. Cirrus sac very broad, short, seldom if ever extending back past ventral sucker; wall of sac thin but definitely muscular. Seminal vesicle long, divided by constrictions into two to several chambers; longer than sac and much convoluted in large specimens. Cirrus much shorter than vesicle, straight or

coiled, with thick muscular wall. Prostate glands up to several hundred in number; fewer in small specimens. Anterior testis near lateral margin on either side of body a little behind seminal receptacle; posterior testis on other side of body or median, near posterior ends of crura in posterior quarter of body, far behind anterior testis in larger specimens and only a little behind it in younger ones; both testes close to ventral surface. Ovary near dorsal surface slightly to one side (either right or left) of median line a short distance behind ventral sucker, which it may touch in some specimens. Seminal receptacle immediately behind ovary; larger than ovary in large specimens. Laurer's canal opening on dorsal surface over intestinal cecum on side of body farthest from ovary. Descending ramus of uterus narrow, tubular, running almost straight back from oötype in dorsal half of body, and turning ventrad near posterior end of body in old specimens or at anterior edge of posterior testis in smaller ones, immediately widening into enormously swollen ascending ramus which runs anteriad, ventral to descending ramus, taking up almost entire width and depth of body in large specimens; ascending ramus dorsal and lateral to testes and sometimes extending under edges of latter, but not ventral to center of testes. Intrauterine eggs up to 5000 or more in large specimens, much fewer in young individuals; ellipsoidal or oblong, operculate, thin-shelled, yellowish; length 63 to 82 (or 100 ?) μ, width 38 to 51 μ; miracidium developing within intrauterine eggs in very old specimens. Vitelline follicles extending in rather narrow band along lateral margins of body from near pharynx to posterior end of body (sometimes falling a little short of the posterior end in young individuals, but always reaching into posterior quarter of body); follicles lateral to esophagus, lateral and ventral to crura throughout length of latter, and meeting in median line of body behind posterior testis. Excretory bladder a broad undivided sac reaching forward immediately under dorsal surface as far as level of seminal receptacle or ovary; opening through short muscular-walled outlet duct to terminal or slightly dorsal excretory pore; main collecting ducts joining bladder on each side near its anterior end; flame cell formula probably $2[(4 + 4 + 4) + (4 + 4 + 4)]$, or at least close to this formula; excretory pattern same as that of *Allocreadium isoporum* and *Crepidostomum cooperi*. Eyespots present, one on each side of pharynx. Miracidium completely ciliated over external surface; rudimentary gut; one pair of flame cells; eyespot in form of two fused pigment cups; cuticular plates lacking. Redia, cercaria, and metacercaria unknown, but cercaria and metacercaria must have eyespots since these are present in adult.

Bunodera luciopercae is the most variable trematode I have studied; because of the great changes in form due to growth of the uterus and to

contraction or extension of the body, specimens differ so much that they could easily be regarded as distinct species except for the existence of specimens showing all intermediate conditions (Figs. 24, 25, 26, 27, 28, 29).

In regard to the life history of *B. luciopercae,* Looss (1894) shows that the cercariae previously assigned to this species by earlier authors, i.e., *Cercaria nodulosa* Linstow 1873 (which Looss says is a synonym of *Cercaria virgula* Filippi 1857) and *Distoma planorbis carinati* Filippi 1857, cannot belong to Bunodera because they lack eyespots. Schuurmans Stekhoven (1931) has reported the metacercaria of *B. luciopercae* from cysts in fishes, but in the absence of any description or recognizable figure his identification must be considered very questionable; the figure he gives does not show any resemblance to Bunodera.

Bunodera sacculata Van Cleave and Mueller 1932

SYNONYMS.—None.

HOSTS AND LOCALITIES REPORTED.—*Perca flavescens,* Oneida Lake, New York; *Lake Okoboji, Iowa.

Through the courtesy of Dr. Van Cleave I have been able to examine whole mounts of some of the specimens on which the original description of *B. sacculata* was based. In addition I have 5 specimens collected by Mr. H. E. Hart from *Perca flavescens* in Lake Okoboji, Iowa, Aug. 1, 1930. I can add only a few details to the original description in the specific diagnosis which follows:

Bunodera sacculata: With the characters of the genus. Length 0.5 to over 2.0 mm.; greatest width usually in post-acetabular region, about one-third of length in most preserved specimens; post-acetabular region becoming swollen and sacculate when uterus is filled with eggs. Suckers about equal. Oral papillae as in *B. luciopercae.* Prepharynx short; pharynx broad and ellipsoidal, length one-fourth to one-third diameter of oral sucker; esophagus longer than pharynx, often convoluted in contracted specimens, with thin muscular wall; crura reaching to level of posterior edge of posterior testis, never extending into posterior one-fourth of body. Genital pore ventral to crural fork or slightly farther forward. Cirrus sac short and broad, with thin muscular wall, reaching back over ventral sucker to center or posterior edge, or sometimes slightly farther; seminal vesicle straight or slightly bent, occupying posterior half or two-thirds of sac; pars prostatica small; cirrus short, thin-walled, muscular; prostate glands much less numerous than in *B. luciopercae,* mostly posterior to pars prostatica; anterior end of cirrus sac eversible. Testes strongly oblique, in anterior half or two-thirds of post-acetabular

region close to ventral surface. Ovary large, near dorsal surface close to posterior margin of ventral sucker, on either side of median line. Seminal receptacle small (possibly lacking; not seen in whole mounts examined to date). Laurer's canal opening on dorsal surface to one side of median line. Uterus running back to extreme posterior tip of body even in young specimens containing less than ten eggs; narrow throughout length in young specimens, becoming wide and sac-like (at least in ascending ramus) and filling almost entire width and depth of body in older ones; metraterm with somewhat thicker and more muscular wall beginning dorsal to ventral sucker. Intrauterine eggs numerous, up to several hundred; operculate; remaining in single-cell stage while in uterus; 65 to 85 μ by 38 to 58 μ with average about 75 by 47 μ in balsam mounts. Vitellaria from pharynx to posterior ends of crura, never reaching into posterior one-fourth of body; follicles dorsal, lateral, and ventral to crura, some extending into intercrural space in dorsal half of body. Excretory bladder a broad undivided pouch reaching forward to posterior end of ovary (according to figure published by Van Cleave and Mueller); nothing known of rest of excretory system. Life history entirely unknown, but presence of eyespots in adult shows that cercaria must have eyespots.

LIFE HISTORIES OF ALLOCREADIIDAE

Although many species and genera have been described and placed in the Allocreadiidae within the last few years, only a few authors have made any attempt to study the life histories of the forms described. *Crepidostomum cooperi* is the only species in the entire family whose life history has been worked out and all stages determined by experiment; the experimental method has been used to work out part of the life cycle in *Megalogonia ictaluri, Hamacreadium mutabile, H. gulella, Sphaerostoma globiporum,* and *Crepidostomum metoecus;* in all other cases the assignment of larval forms to specified species has been based on morphological resemblance, so that most of the life histories are still open to doubt, though tentatively acceptable until contradictory evidence is available.

The redia and type of cercaria are known for four of the nine species of Crepidostomum and for *Megalogònia ictaluri,* while nothing is known of the life cycle of Bunodera. Little is known of the development of other Allocreadiidae, but the available evidence indicates that there are three types of life cycle among the genera which have been assigned to this family by recent authors: (1) the type represented by

Allocreadium, Crepidostomum, and Megalogonia, in which the cercaria is an ophthalmoxiphidiocercaria developing in rediae in Sphaeriidae and the metacercaria encysts in crustacea, aquatic insects, or molluscs; (2) the type represented by Hamacreadium, Plagioporus, and Sphaerostoma, in which snails are the molluscan hosts and the cotylocercous cercaria, with stylet but without eyespots, develops in sporocysts; the metacercaria is always encysted, but the type of intermediate host differs greatly in the different species; (3) the type represented by Lepocreadium and Pharyngora, in which the cercaria has a long setiferous tail and develops in rediae in snails; in this type the metacercaria of each species may live in a great variety of hosts, but does not encyst. Of course there may be other types of life history in the family, for nothing is known of the larval stages in more than two-thirds of the genera and in an even larger proportion of the species.

The cercaria of Bunodera is unknown, but it is safe to assume that the cercaria has eyespots, since they are still present in young adults; recently Schuurmans Stekhoven (1931) has reported the metacercaria of *B. luciopercae* from cysts in fish, but his identification is at least doubtful. Palombi (1929) has described the metacercaria of *Helicometra fasciata* from Mediterranean shrimps of the genus Leander. Parts of the life cycles of two or possibly three other species of Allocreadium, in addition to *A. isoporum,* are now known. According to Lühe (1909) the *Distoma agamos* Linstow found in Gammarus and Asellus is probably the metacercaria of *Allocreadium transversale,* I have found the metacercaria of *A. ictaluri* Pearse encysted in the mantle of various Unionidae and Sphaeriidae, and Stafford (1931) has reported "adult" specimens of "*Allocreadium tumidulum*" from *Hexagenia variabilis. Peracreadium tumidulum* is a parasite of marine fish, so it is hardly possible that Stafford's specimens belong to this species. Professor Ward has specimens of metacercariae found encysted in the foot of Unionidae and in Gammarus which I have identified as *Anallocreadium armatum.* The life histories of *Hamacreadium gulella* and *H. mutabile* were described by McCoy (1929, 1930), the life histories of *Plagioporus siliculus* and *P. virens* by Sinitsin (1931), the life history of *Sphaerostoma globiporum* by Sinitsin (1905, 1907), and the life history of *Allocreadium isoporum* was indicated by Looss (1894) and Linstow (1897). The cercaria and metacercaria of *Lepocreadium album* and *Pharyngora bacillaris* have been reported by many authors, and a critical review of the literature on these forms has been presented by Dollfus (1925). Progenetic metacercariae of *Plagioporus cooperi* (Hunter and Bangham 1933) were found in mayfly nymphs by Cooper (1915).

related to the Opecoelidae. I do not believe there is sufficient reason for the proposed placing of Opecoelidae in the family Allocreadiidae as a subfamily, but this question is outside of the scope of the present paper.

In the present state of knowledge statements of relationships within the family or of relationships to other families are statements of opinion only; until more is known of the structure, especially of the much neglected excretory system, and of the life histories of all the genera considered, any attempt at "revising" the classification is useless. The present chaotic condition of the classification of the Digenea is preferable to an iron-bound artificial system, for at least the present condition is stimulating to research and is not conducive to preconceived ideas based on paper relationships.

SUMMARY

1. Detailed, corrected generic diagnoses are given for Crepidostomum, Megalogonia, and Bunodera.

2. Acrolichanus cannot be adequately distinguished from Crepidostomum, so the generic name Acrolichanus is suppressed.

3. Bunodera belongs in the family Allocreadiidae close to Crepidostomum and Megalogonia; all three genera are closely related to Allocreadium; the three papillose genera probably represent one branch of the ancestral stem from which Allocreadium arose.

4. *Crepidostomum farionis* is reported from new hosts and localities; its known range now extends from New England to Alaska in North America, while in the Eastern Hemisphere it is known in northern Europe and the Pacific coast of Siberia.

5. *Crepidostomum ussuriensis* Layman 1930, *Stephanophiala vitelloba* Faust 1918, and *Stephanophiala transmarina* Nicoll 1909 are synonyms of *C. farionis* (O. F. Müller 1784).

6. *Crepidostomum ambloplitis* Hopkins 1931, *C. solidum* Van Cleave and Mueller 1932, and *C. Faust* Hunninen and Hunter 1933 are synonyms of *C. cooperi* Hopkins 1931.

7. New hosts and localities are reported for *C. cooperi,* showing that the species is abundant and widely distributed in central and eastern North America, and a detailed description is given, including the excretory system.

8. The life history of *C. cooperi* has been worked out. The metacercaria has a pigmented eyespot; the cercaria is a slender-tailed ophthalmoxiphidiocercaria developing in rediae in *Musculium transversum* and *Pisidium* sp.; the metacercaria is encysted in the abdominal cavity of Hexagenia nymphs and adults.

9. New hosts and localities are reported for *C. cornutum* (Osborn)

and a detailed description of structures previously neglected or misinterpreted is given, including the excretory system. A stylet has been found in the metacercaria for the first time, showing that the cercaria is an ophthalmoxiphidiocercaria.

10. Faust's description of *C. illinoiense* Faust 1918 is corrected.

11. *C. hiodontos* Hunter and Bangham 1932 is a synonym of *C. illinoiense*.

12. A few details are added to the original description of the adult *C. isostomum* and the redia, cercaria, and metacercaria probably belonging to this species are described.

13. *Crepidostomum auriculatum* (Wedl 1857) is the correct name for *D. auriculatum* Wedl 1857; a diagnosis of the species is given to include the information presented by Skworzoff (1927, 1928).

14. *Acrolichanus similis* Wisniewski 1933 is probably a synonym of *C. auriculatum*.

15. *Crepidostomum lintoni* (Pratt 1901) is apparently the correct name for *D. auriculatum* Wedl (?) of Linton 1898 = *D. petalosa* Lander 1902 = *Acrodactyla petalosa* = *Acrolichanus petalosa* = *Bunodera lintoni* Pratt 1901. A corrected description of the species is given.

16. A corrected, detailed account of *Megalogonia ictaluri* Surber 1928 is given, including the excretory system, and a few new hosts and localities are reported.

17. The miracidium, redia, cercaria, and metacercaria of *Megalogonia ictaluri* have been found. The miracidium has a pigmented eyespot; the cercaria is a slender-tailed ophthalmoxiphidiocercaria developing in rediae in *Musculium transversum;* the metacercaria is encysted in the gills of Hexagenia nymphs.

18. A few details are added to the original description of *B. sacculata* and it is reported for the first time from Iowa.

19. The known life histories of Allocreadiidae are compared; there are three types of life history within the family. Allocreadium, Crepidostomum, Megalogonia, and possibly Bunodera have an ophthalmoxiphidiocercaria developing in rediae in Sphaeriidae and encysting in various invertebrates.

20. The excretory systems of *Crepidostomum cooperi, Crepidostomum cornutum, Megalogonia ictaluri,* and *Allocreadium ictaluri* Pearse have been worked out in detail and found to have a common pattern with *Allocreadium isoporum* Looss as described by Looss. Faust's formula for Allocreadium is wrong, being founded on a mistaken interpretation of Looss' work. The fundamental formula for Crepidostomum, Megalogonia, and Allocreadium is $2[(2+2+2)+(2+2+2)]$, which is modified by additional divisions of flame cells in some species.

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EXPLANATION OF PLATES

Abbreviations

c	common vitelline duct	p	primordia of testes
cy	cystogenous glands	r	seminal receptacle
d	oviduct	s	seminal duct from receptacle
f	fertilization chamber	sg	stylet gland
g	genital anlage	t	transverse vitelline duct
i	intestinal cecum	u	uterus
l	Laurer's canal	ua	ascending ramus of uterus
o	ovary	ud	descending ramus of uterus
oo	oötype	v	vitellaria

All figures were drawn with the aid of a camera lucida. The scale line represents 0.2 mm. in Figures 1, 2, 3, 5, 6, 9, 10, 11, 12, 13, 14, 15, 16, 19, 22, 23, 24, 25, 26, 27, 28, 29; 0.05 mm. in Figures 4, 7, 17, 18, 20 (and 21), and 30; and 0.02 mm. in Figure 8.

PLATE I

FIG. 1.—*C. cooperi,* metacercaria drawn from living specimen, ventral view.

FIG. 2.—*C. cooperi* adult, mounted in extended condition, ventral view.

FIG. 3.—*C. cooperi* adult, mounted in contracted and slightly flattened condition, ventral view.

FIG. 4.—*C. cooperi* miracidium in egg, drawn from living specimen, dorsal view.

FIG. 5.—*C. cooperi,* young redia with eyespot, living specimen.

FIG. 6.—*C. cooperi,* mature redia containing cercariae, living specimen.

FIG. 7.—*C. cooperi* cercaria, living specimen, ventral view; glands omitted on left side, excretory tubes omitted on right; *a,* stylet, more enlarged, lateral view.

FIG. 8.—Comparison of stylets of cercariae; *a,* stylet of *C. cooperi; b,* stylet of *Megalogonia ictaluri.*
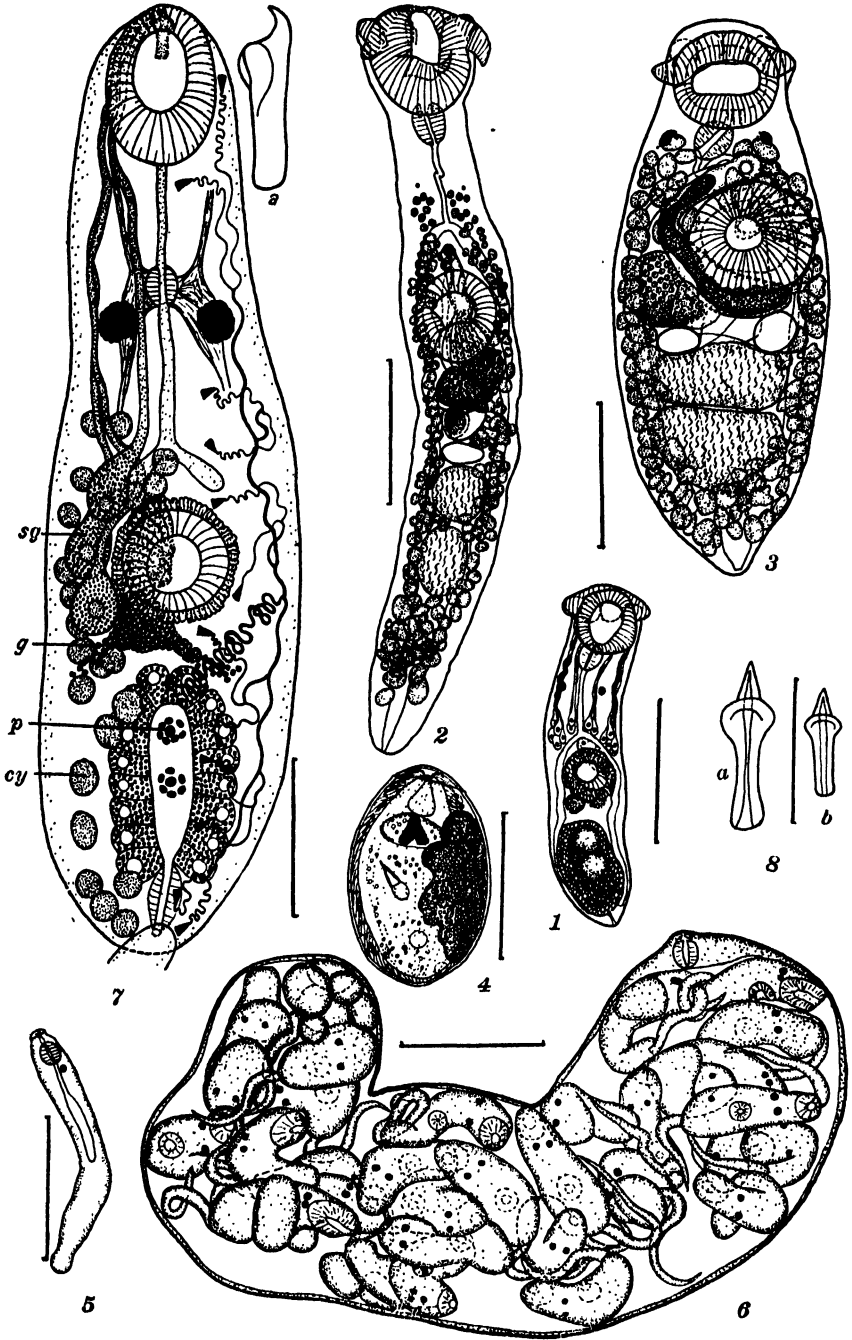
PLATE I

PLATE II

FIG. 9.—*C. cooperi,* redia containing daughter rediae, living specimen.

FIG. 10.—*C. farionis,* adult; Faust's type specimen of *"Stephanophiala vitel-loba,"* whole mount, ventral view.   •

FIG. 11.—*C. metoecus* adult; specimen from Vienna Museum, labeled *"Crepi-dostomum metoecus* Braun—Type," ventral view.

FIG. 12.—*C. metoecus* adult; specimen from Berlin Museum (vial 5774), dorsal view.

FIG. 13.—*C. metoecus* adult; specimen from Berlin Museum (vial 5774), lateral view.

FIG. 14.—*C. isostomum* (?), redia containing one cercaria, whole mount.

FIG. 15.—*Megalogonia ictaluri,* adult, lateral view, whole mount.
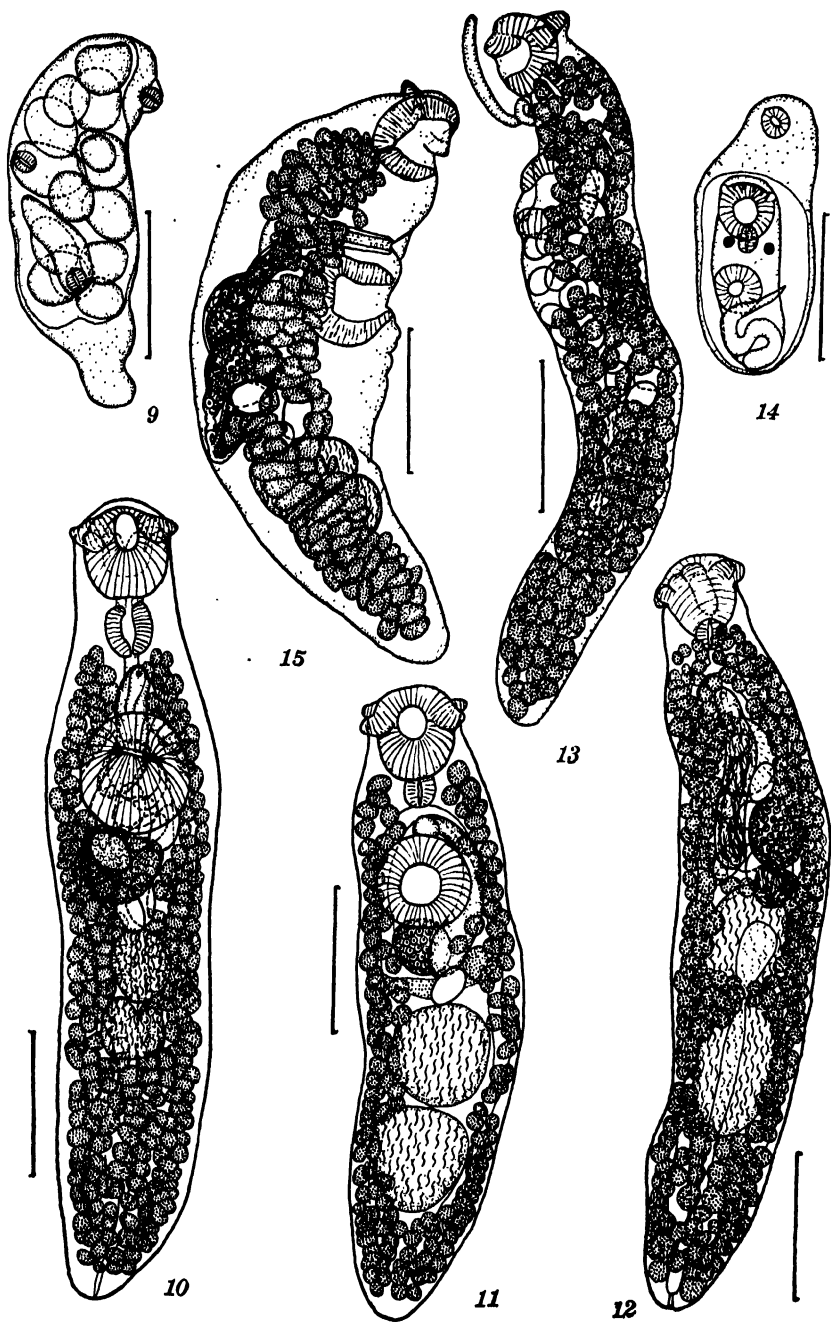
PLATE II

PLATE III

FIG. 16.—*C. illinoiense* adult; Faust's type specimen, whole mount, dorsal view.

FIG. 17.—*C. illinoiense* adult; female reproductive organs, graphic reconstruction from transverse sections, dorsal view.

FIG. 18.—*C. illinoiense* adult; diagrammatic cross section through female reproductive organs.

FIG. 19.—*Megalogonia ictaluri* adult, whole mount, dorsal view.

FIG. 20.—*M. ictaluri* miracidium in egg, living specimen, dorsal view; extended.

FIG. 21.—*M. ictaluri* miracidium in egg, living specimen, lateral view; contracted.

FIG. 22.—*Bunodera lucioperiae* adult, diagrammatic cross section through female reproductive organs.
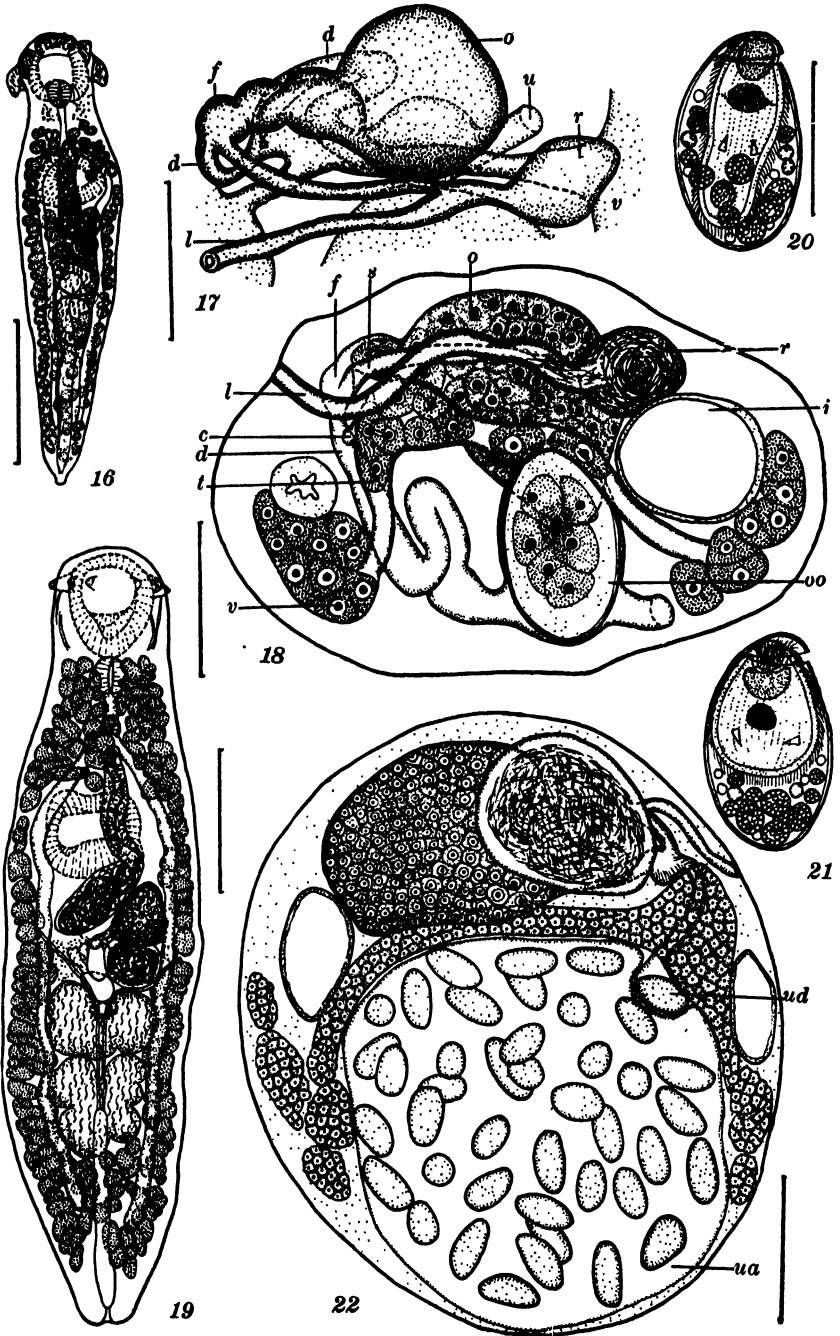
PLATE III

PLATE IV

FIG. 23.—*Megalogonia ictaluri* metacercaria, living specimen, slightly flattened; ventral view.

FIG. 24.—*Bunodera luciopercae* adult, specimen from Berlin Museum (vial 1568), lateral view.

FIG. 25.—*B. luciopercae* adult, specimen from Berlin Museum (vial 1568), lateral view.

FIG. 26.—*B. luciopercae* adult, specimen from Berlin Museum (vial 1568), dorsal view.

FIG. 27.—*B. luciopercae* adult, specimen from Königsberg Museum, dorsal view.

FIG. 28.—*B. luciopercae* adult, specimen from Königsberg Museum, lateral view.

FIG. 29.—*B. luciopercae* adult, American specimen, ventral view; contains several thousand eggs, but for the sake of clearness only one egg is shown; the rest of the uterus is indicated by stippling.

FIG. 30.—*B. luciopercae* adult; flame cells as seen in sectioned material.

PLATE IV

INDEX

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ILLINOIS BIOLOGICAL MONOGRAPHS

EDITORIAL COMMITTEE

EVOLUTION OF FOLIAR TYPES, DWARF SHOOTS, AND CONE SCALES OF PINUS

With Remarks Concerning Similar Structures in
Related Forms

WITH THIRTY-TWO TEXT-FIGURES

BY

CLIFTON CHILDRESS DOAK

ACKNOWLEDGMENT

CONTENTS

I. INTRODUCTION

A. Review of Literature

Since the dawn of botany as a science, the Gymnosperms have been of special interest; and the genus *Pinus*, because of its wide distribution, its economic importance, and its highly specialized dwarf shoots, has probably attracted more investigators than any other genus among gymnosperms. Hundreds of special papers dealing with this subject have appeared, the most important of which will be cited in connection with the special topics of which they treat. Numerous general works either include *Pinus* or deal with this genus alone. A modern and nearly complete list of the general works will be found in *A Handbook of Coniferae,* by Dallimore and Jackson (24).* Since the present paper deals with both the foliar and axial systems of pines, much of this extensive literature has either a direct or an indirect bearing on the present problem.

Some of the most important early works in the field of pines were done by Lambert (50) and Engelmann (30) from whose works early literature lists may be obtained.

The embryo and cotyledons have been the subject of special studies or have been included in the works of Goethe (40), Richards (72), Engelmann (30), Daguellion (23), Tubeuf (93), Masters (57), Buchholz (13, 14), and others.

The seedling stages were treated by Menge (62), Beissner (5), Masters (57), Hill and DeFraine (41), and numerous others, while the buds and bud scales have been made the objects of special investigations by a long list of workers including Schumann (80), Lord Avebury (54), and Masters (57).

The interpretation of the cone scales has been the subject of a controversial and almost endless literature. Some of the chief contributors in this field are Robert Brown (12), Alexander Braun (11), Baillon (2), Sachs (75), Willkomm (101 and 102), Celakovský (20), Schleiden (78), Parlatore (68), Velenovský (97), Von Mohl (99), Strasburger (87), Aase (1), Saxton (76), and a host of others.

The literature dealing with the dwarf shoot is not so extensive. Important morphological contributions have been made, however, by Masters (57), Thompson (91), Schneider (79), and a few others, while important contributions from the fossil records have been made by Jeffrey (46) and Seward (81).

*Numbers following names of authors refer to items in the Bibliography at the end of this paper.

B. The Problem

During the accumulation of the mass of literature now available much has been learned of the genus *Pinus* and its affinities. Much of this information, however, exists as detached fragments. The great need is for consolidation, supplementary investigation, and re-interpretation. With these needs in view the present work was undertaken. As the investigation progressed it became obvious that a detailed study of the ontogeny and morphology of the entire axial and foliar systems would contribute materially to a better interpretation of the phylogeny and affinities of the genus. The problem as thus broadened involves consideration of a highly
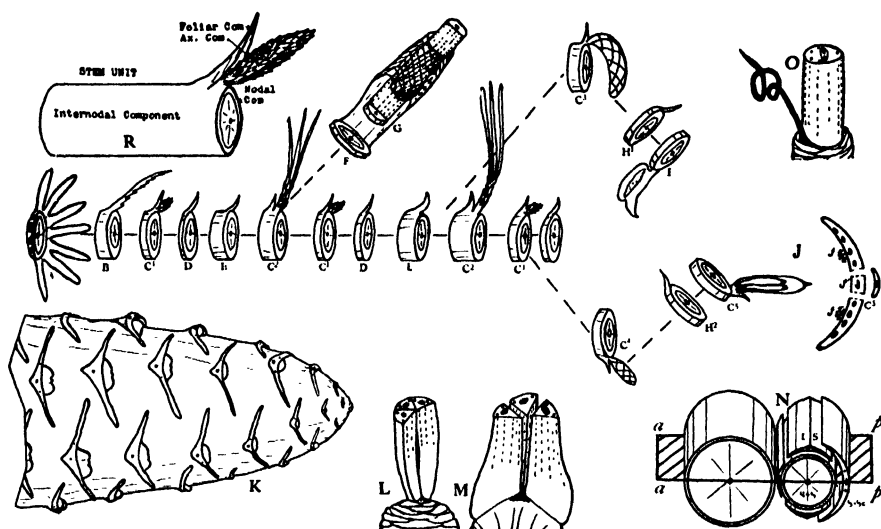
Fig. 1.—Stem units of a pine (and miscellany).

A. Cotyledonary units.
B. Simple-leafed juvenile unit.
C. Fertile units.
  C¹. Branch bud unit.
  C². Dwarf shoot unit.
  C³. Staminate cone unit.
  C⁴. Ovulate cone unit.
  C⁵. Seed scale unit.
D. Bud scale unit.
E. Sterile bract unit.
F. Sheath scale unit.
G. Functional leaf or needle unit.
H¹ and H². Involucral scale units.
I. Microsporophyll unit.
J. Megasporophyll unit.
K. Semi-diagrammatic view of a stem tip during deposit of fertile units. The subtending scales have been removed in order to show the young dwarf shoots.

L. Diagram of denuded dwarf shoot of *P. Strobus* showing base of growing leaves. The sheath scales have been removed.
M. Same showing mature leaves and well-formed "pulvinus."
N. Diagram of axial plane passing through both the long shoot and the dwarf shoot. Lateral and subtending scales are also shown.
O. A two-needled dwarf shoot with one of the needles aborted.
R. Diagram showing components of a fertile stem unit.

specialized, polymorphic branch system and an even more highly complex system of specialized structures which are the morphological equivalents of leaves.

Since the acceptance of the idea that the fascicle is borne on a dwarf shoot, it has been known that pines exhibit an extreme case of dimorphism of the vegetative branches. The possession of specialized, deciduous, dwarf shoots in contradistinction to the long shoots, is now universally accepted as the chief distinguishing character of the pines.

The modified branches which serve as axes for the staminate and ovulate cones respectively are not of the same order and are not, therefore, homologous.

According to the widely accepted "Brachyblast Theory," the seed scale also represents a modified branch; hence the branches of *Pinus* are not dimorphic but polymorphic, there being a total of five types as follows: (1) long shoot; (2) dwarf shoot; (3) staminate cone axis; (4) ovulate cone axis; and (5) seed scale axis.

In addition to this complex branch system, there are developed in the course of the ontogeny of each pine tree at least eleven types of specialized leaf structures. These were in part described by Engelmann (30), who recognized seven types exclusive of the sporophylls. Dufrenoy (27) pointed out the fact that in some ancestors of pine, the undifferentiated leaves likely served the triple functions of spore formation, carbon assimilation, and protection of the meristematic tips. By way of specialization to serve one of these functions or some combination of them, the organs here listed, in order of their ontogenetic appearance, have evolved.

1. Cotyledons (Fig. 1 A).
2. Simple, primary or juvenile leaves (Fig. 1 B).
3. Bud scales (Fig. 1 D).
4. Sterile bracts of the main axis (Fig. 1 E).
5. Fertile or subtending bracts of the main axis.
    a. Subtending branch buds (Fig. 1 C^1).
    b. Subtending short shoot (Fig. 1 C^2).
    c. Subtending staminate cones (Fig. 1 C^3).
    d. Subtending ovulate cones (Fig. 1 C^4).
6. Fascicle sheath scales (Fig. 1 F).
7. True or needle leaves (Fig. 1 G).
8. Involucral bracts for the cones.
    a. For staminate cones (Fig. 1 H^1).
    b. For ovulate cones (Fig. 1 H^2).
9. Microsporophylls (Fig. 1 I).
10. Cover scales or bracts for the seed scales (Fig. 1 C^5).
11. Megasporophylls (Fig. 1 J).

The scope of the problem as outlined here is so broad that the present paper must necessarily include numerous separate short investigations undertaken either to supplement and round out data already available or to bridge the gaps between bodies of existing knowledge. In the light of these investigations, the author hopes to summarize and re-interpret some of the controversial questions raised by the work of other investigators. Obviously, too, any consideration of phylogenetic relationships must involve other genera, both paleontological and extant.

C. Materials and Methods

The materials for this study were taken from pines of about thirty-five species gathered from widely separated points throughout the United States and neighboring islands. Many European and Asiatic forms which are now growing under cultivation in America are included. The most detailed studies were made on *P. sylvestris* L., *P. Laricio* var. *austriaca* End., *P. cembroides* var. *monophylla* Voss., *P. taeda* L., *P. Pinaster* Ait., *P. palustris* Mill., and *P. Strobus* L. In all of these species the observations extended over either two or three growing seasons.

Seeds, buds, and other parts were dissected under a binocular dissecting microscope; and those parts which the binocular revealed as being of possible histologic interest were later imbedded and sectioned.

For the major subdivisions of the *Conifereae*, the writer has followed the classification used by Coulter and Chamberlain (22). The specific names of the various pines have been taken from Dallimore and Jackson (24).

D. Definitions of Terms

A *stem unit* is considered in this paper to be an internode, together with the node and nodal appendages at its distal extremity (Fig. 1 R). It consists of an allotted portion of a stem (internodal component), a poorly defined node, a modified or unmodified leaf (foliar component) which may or may not subtend an axillary outgrowth (axillary component). A unit without an axillary component is said to be *sterile*.

The term *node* is used in its usual sense; but since the term *multinodal* has been used (see Shaw, 82) to describe the annual growths which show more than one period of deposit in a single season, the term is retained in this sense even at the risk of some confusion. It is to be remembered, however, that the term *multinodal* refers not to a plurality of nodes but to a plurality of periods of deposit.

In the literature the terminal bud of the dwarf shoot, because of its position with reference to the needles, has been termed the *interfoliar* bud in which sense the term is here retained.

The term *dwarf shoot* is applied to the modified branches which in the literature are often called by various other names such as spur shoot, short shoot, and brachyblast. The term *fascicle* is reserved for the tuft of needles on a dwarf shoot and is thought of as being separate from the sheath of scales (*fascule sheath*) around the needles.

By *deposit* is meant the instant of earliest recognition of a primordium.

The term *bud scale* is used in its restricted sense 'and is applied to those closely spaced, sterile-axiled, scale-like, primary foliar organs which serve only as protective cover for the buds.

By *extension* is meant the enlargement of a structure to its final size (second growth phase). The *year's growth* is that portion of a long shoot of which the units are extended during a single growing season.

The term *perforation* is applied to the growth of other parts through a scale (Fig. 11 C, C', and D'). The term *axial plane* is applied to a plane passing through the long axes of both a dwarf shoot and the long shoot to which the short shoot under consideration is attached (Fig. 1 N, a-p).

A primordium formerly present but no longer appearing is considered to have been *suppressed*; if the rudiment appears and is then lost without differentiation of vascular tissues, the structure is said to be *incorporated*. If the structure represented by a primordium loses its identity as a separate organ but, as a constituent of a connate structure, differentiates a separate vascular supply, it is considered to have been *welded* into a now *compound* structure.

The seed scale can be shown to consist of more than one foliar unit; for this reason the term *sporophyll* is applied to the morphological spore-bearing leaf which forms only a part of the seed scale. The term *seed scale*, therefore, is reserved for the entire seed-bearing structure.
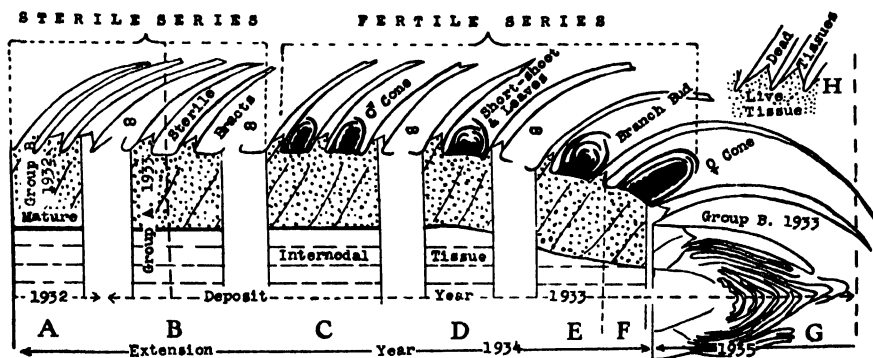
Fig. 2.—Diagram of a compound winter bud of pine, showing condition of units, order of deposit, and order of extension.

II. THE VEGETATIVE LONG SHOOT

A. SIMPLE LEAVES OF THE LONG SHOOT

The order of appearance of the various units which make up a pine tree has been given above. We shall now consider each type of unit in the light of the observations made during the present study. The first leaves to appear are always of the simple type. These are usually glaucous and, with the exception of the cotyledons, have toothed margins (Fig. 5 C and Fig. 6 C) even in species whose functional leaves are entire. They are broadened laterally, especially at their bases. They are keeled and never grow for long periods from zonal meristems, as do the regular needles, but mature all their tissues at approximately the same time. Simple leaves are not confined to the vegetative long shoots but occur also on dwarf shoots and even on the cone axes. In the course of the present work, during which hundreds of branches were examined, a close watch was kept for possible simple leaves. Numerous cases were found which, when analyzed, fell under one of the types listed below.

1. Cotyledons

The first simple leaves to appear are the cotyledons about which there has accumulated an extensive literature. It is generally agreed that the cotyledons are conservative in characters and, since they themselves are simple, are indicative of a simple-leaved ancestor for the genus *Pinus*.

As early as 1817 Goethe (40) argued that if a leaf is not to be thought of without a node or a node without a bud, the cotyledons, since they are leaves, mark the first node of a plant. He accounted for their cyclic arrangement and sterile axils by assuming a phylogenetic loss of both internodes and axillary buds. The essential correctness of these interpretations is borne out by the occasional assumption of a weak spiralled arrangement as reported by Buchholz (13, 14), or by the occurrence of buds in the axils of the cotyledons as found by Richards (72).

In following the early ontogeny of the cotyledons, Buchholz (13) has shown that the meristem of the stem tip arises in the embryo before the cotyledonary primordia are laid down. This differentiation of meristem for the plumule marks the beginning of the long shoot, and the appearance of the cotyledonary primordia upon it marks the beginning of its first foliar appendages. In the papers just cited, Buchholz shows that two or more cotyledonary primordia often "fuse" and give rise to a single cotyledon (Fig. 7 C, D, E, and F). He describes broad cotyledonary primordia of possible double nature and also undoubted double primordia which, without leaving a trace of their former bivalence, develop into simple structures. My own investigations have revealed similar processes

in *P. taeda.* They are probably of common occurrence among other poly-
cotyledonous forms. Buchholz and Old (16), in their work on embryos
of a close relative of *Pinus,* express the view that the cotyledonary tubes
observed by Hill and DeFraine (41, 42) in the seedling stages of *Cedrus
atlantica* were produced by intercalary growth during germination. The
degree of adhesion attained in the formation of such tubes indicates that
fusions can occur either early or late in cotyledonary ontogeny and that
the union can be either complete (primordia incorporated) or partial
(structures welded).

In order to bring about incorporation the primordia are deposited as
is normal for growing points. Meristematic activity, however, instead of
being confined to these—which would result in the production of separate
organs—spreads laterally and recedes toward the base until all the inter-·
vening and subjacent tissues are involved. Two or more adjacent pri-
mordia are thus lifted up by a common (intercalary) growth. At first
the resulting compound structure has as many growing points as there
were constituent primordia. Some of the points, however, are soon in-
corporated and their separate identity is lost. Hence the mature organ
is usually univalent, and there is no trace of the double or triple nature of
its early ontogeny. From such evidence obtained in work on the embryos
of *P. Banksiana,* Buchholz concludes that there is in this species a distinct
tendency to reduce the cotyledons.

That this phenomenon is not confined to *P. Banksiana,* and that the
incorporation of one organ by another is not always complete, is shown
by the frequent occurrence of double, bivalent, or welded cotyledons as
described by Hill and DeFraine (41, 42).* These workers show that the
union may involve a part or all of the cotyledons, the latter condition pro-
ducing a hollow cylindrical cotyledonary tube. Such tubes were reported
as occurring regularly in five species of pines and in several other gymno-
sperms.

Since the results just described are nothing more than different ex-
pressions of the same fusion phenomenon, it is significant, but not sur-
prising, that double cotyledons and occasional cotyledonary tubes are
found in the same species. What is more significant is that, for those
pines (*P. contorta* var. *Murrayana,* and *P. montana* var. *gallica*) showing
both fused cotyledons and occasional cotyledonary tubes, the total number
of maturing cotyledons is far lower than occurs in pines generally. Of

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*Curiously enough these workers interpreted the partly divided cotyledons as evidence
that, by division, the dicotyledonous condition, which they held to be primitive, was giving
rise to polycotyledony. As pointed out by Coulter and Chamberlain, however, the partly fused
condition can be used with equal force to show that by fusion of members the primitive poly-
cotyledonous condition is giving rise to the condition of dicotyledony. The fact that primordia
were observed to fuse, not only in *Pinus,* but in several other polycotyledonous genera, makes
it probable that polycotyledony is primitive and dicotyledony derived, which is the view of the
present writer.

all species studied by Hill and DeFraine, the prevailing cotyledonary numbers ran -12-11-10-9-9-8-7-6-4-4-4-, and yet the number occurring in the two pines which showed both these conditions was in each case four, the lowest number in the series. These facts are strongly suggestive of *fusion and incorporation as the means by which the reduction to this low number has been accomplished.* This is in keeping with the theory of a generalized tendency toward reduction which Coulter and Chamberlain (22) have set forth for all gymnosperms.

It is apparent that the ontogeny of adjacent cotyledonary or other primordia can follow any one of three courses. The usual course is for each primordium to grow into a separate structure; this, of course, involves no reduction. Either of the other methods, however, results in fewer mature organs than beginning primordia. If, by intercalary growth, two or more primordia are lifted on a common structure, as described above, and each constituent later differentiates its own vascular supply, the effect is to produce a reduced number of organs which are clearly bivalent, or connate, as are the cotyledons of a cotyledonary tube. However, since the vascular supply to pine cotyledons is usually simple, this cannot be the means by which cotyledonary reduction is being accomplished in *Pinus*.

The third possibility involves reduction by elimination of primordia through *complete incorporation* as described above.

The tendency toward the elimination of foliar primordia by *meristematic recession* and *incorporation* is not confined to the cotyledons but manifests itself at many points in the ontogeny of a pine tree, and, as will be shown later, it is by this process that the stem tip and extra leaf primordia are eliminated from the dwarf shoots of *P. cembroides* var. *monophylla*. The fusion of parts of the Abietineous cone scale and the elimination of parts from this structure are also explainable on similar grounds. For these reasons it is not alone the *evidence of reduction* but also the *manner of reduction* which assumes importance in the present paper.

2. Juvenile and Traumic Simple Leaves

Above the cotyledons the seedlings of all pines are at first clothed with simple leaves, as shown by Menge (62), Coulter and Chamberlain (22), and many others. The simple leaves are spirally arranged along the long axis, a character which is held in common with all *Abietineae*.

The simple leaves are followed eventually by scales and other specialized foliar organs (Fig. 1). The early botanist rightly attached significance to this sequence and used it as an argument for the derivation of specialized leaves from the simple type. Beyond the seedling stages,
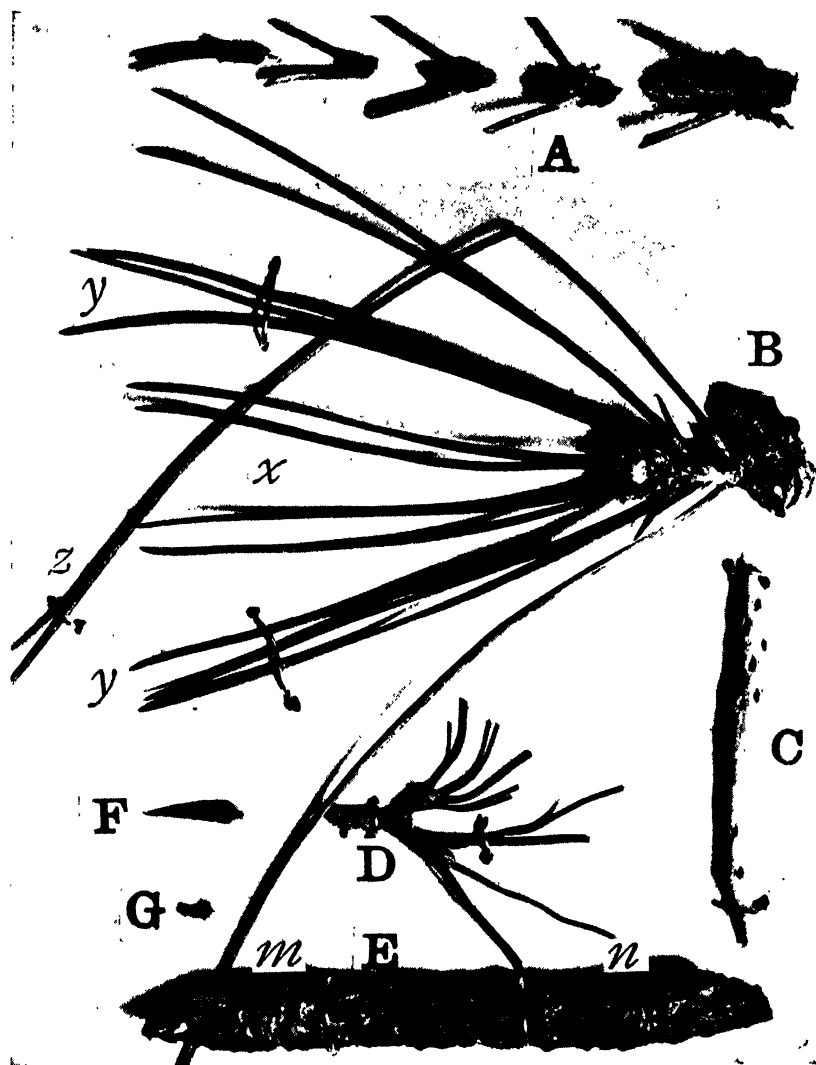
FIG. 3.—Proliferated dwarf shoots (and miscellany).

A. Interfoliar buds of *P. Laricio.*
B. Proliferated fascicle of *P. Laricio* with simple subtending leaves, withered original needles (*z*) and three-needled fascicles (*y*).
C. Xylem cylinder from a young twig showing naked portion in position of former bud scale scar.

D. Interfoliar buds of *P. Strobus.*
E. An annual growth node of *P. Laricio* showing scars of the different units; *m* and *n* represent bud scale scars.
F. Simple green leaf from *B.*
G. Shed lateral scale from *B.*

simple leaves occur most commonly as responses to traumic and nutritional stimuli (53, 54). An extensive examination of almost any pine material, however, will reveal a few spontaneous simple leaves for the transformation of which no known cause can be ascribed.

FIG. 4.—Dwarf shoots.

A. Six-needled dwarf shoot from *P. palustris.*
B. Normal three-needled dwarf shoot from *P. palustris.*

C. Normal dwarf shoot from *Cedrus.*
D. Abnormal dwarf shoot from *P. palustris.*

During the first year of the present work several hundred buds were removed from trees in the vicinity of Urbana, Illinois. The twigs from which the terminal buds were removed usually responded in one of two ways. They either pushed out and extended the units in the lateral buds which ordinarily would have remained dormant, or they proliferated new branches from the old dwarf shoots (Fig. 3 A and B). Often new branches came from both sources.

In those cases involving the forced extension of a dormant bud, the subtending foliar components, which had for a time served as resting primordia, seemed during this service to have had the future behavior of their tissues fixed, because after extension these in all cases formed scales
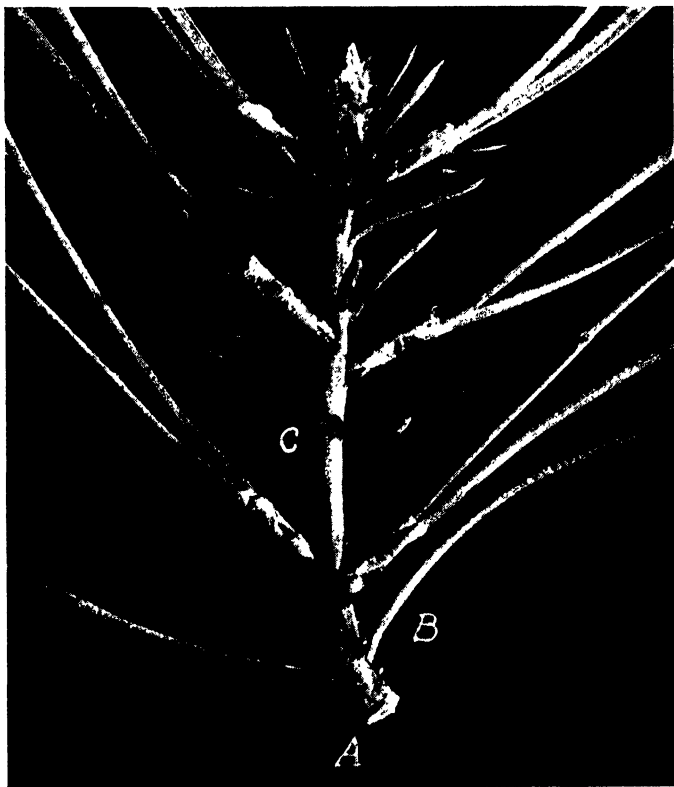
FIG. 5.—Proliferated dwarf shoot of *P. pinaster.*
A. Dwarf shoot.   C. Simple green leaves with
B. Withered original leaves.   toothed margins.

of the usual type. As previously reported by Lloyd (53), those subtending structures which were deposited and extended during the same season were, however, transformed into simple leaves (Fig 3 B and F and Fig. 5 C). Those cases in which a proliferation grew from the old dwarf shoots will be further described under the section dealing with the growing point.

It is a common observation that pines, when heavily fertilized, irrigated, or otherwise subjected to unusually favorable conditions, will pro-

duce simple leaves. Sometimes this occurs naturally (Büsgen, 17; Goebel, 38), especially in southern climates. So frequently does it occur in *P. cubensis* which grows on the Isle of Pines, surrounded as it is by the warm waters of the Caribbean, that at one time efforts were made to set up a new species (Rowlee, 74) based upon this character.

In certain conifers, notably *Juniperus* and *Chamaecyparis,* varieties have been established which, when propagated vegetatively, maintain the juvenile leaves throughout life. In horticultural literature these are
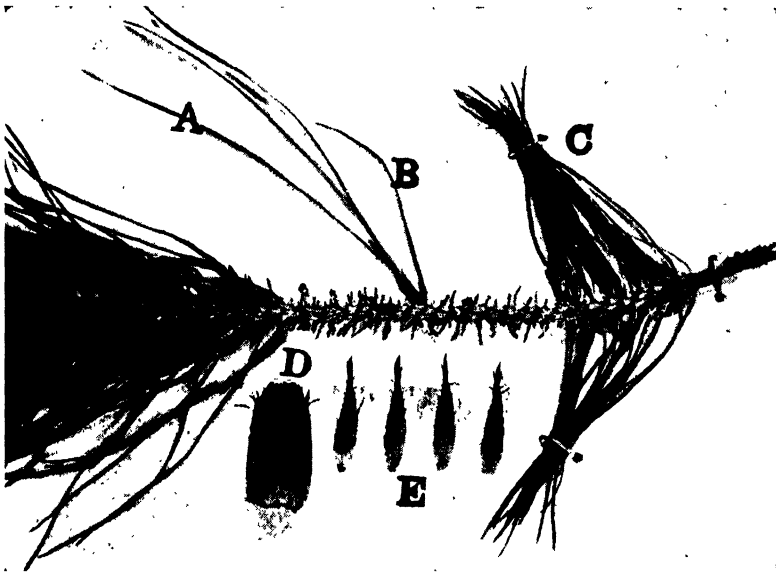
Fig. 6.—Twig from retinosporous pine (and miscellany).

A. The only fascicle on the twig.
B. Simple subtending leaf.
C. Simple sterile leaves a part of which
   have been clipped away in order
   to show the fascicle, *A*.

D. Winter bud of *P. palustris.*
E. Scales from same showing inter-
   lacing fibers.

spoken of as retinosporous varieties. The attempt to obtain a pine with simple leaves throughout has been only partly successful. It is not so unusual, however, to find branches or entire young trees on which the simple leaves predominate (Fig. 6). Several such trees are now growing in the greenhouses at the University of Chicago while hundreds of such branches may be found on trees growing at College Station, Texas. Hochstetter (43) describes as "incomparably beautiful" a simple-leafed variety of *Pinus* which he, for a time, was able to maintain but which unfortunately perished after a few years.

The wide differences between simple leaves in general and the foliar organs now found on *Pinus* serve to emphasize the extreme foliar specializations of the genus. At the same time the simple leaves furnish us with evidence regarding a type of leaf from which, or through which, the numerous kinds of modern and highly specialized foliar organs of *Pinus* have evolved.

B. Bud Scales, Sterile Bracts, and Subtending Scales

Of the eleven kinds of foliar components mentioned above, six are scale-like. These are (1) bud scales, (2) sterile bracts of the main axis, (3) fertile bracts of the main axis or subtending scales, (4) fascicle sheath scales, (5) involucral bracts of the cones, and (6) cover scale or bracts for the seed scales. The first three of these are found on the vegetative long shoot, while the involucral bracts, fascicle sheath scales, and cover scales are borne on branches of a second order.

Like the simple leaves treated above, the scales on the main axis are primary foliar organs. Of them Büsgen (17) says:

Observation and experiment alike teach that the bud-scales and leaves actually originate in essentially similar rudiments whose later development is decided by their surroundings, i.e., their relationship to other parts of the whole shoot competing with them in growth and nutrition and to the climatic conditions.

As pointed out above the early removal of the leaves at the tip of a shoot causes buds actually destined for development the following year to extend in the year of their formation, and in this event true leaves are formed from primordia which, in the ordinary course of things, would have become scales.

This behavior is not surprising, for, as pointed out by Jeffrey (46) and Fontaine (34), ancestral pines probably had simple leaves where we now find the scale series and in addition bore fascicles similar to those now found on pines. The transformed simple leaves, therefore, may be looked upon as reversions.

The various kinds of scales present no fundamental morphological differences. The units on which they are borne are here separated into groups on the basis of (1) time of deposit, (2) amount of ultimate extension of the internodal component, and (3) presence or absence of axillary components. Because of the morphological similarities throughout the series, the description of bud scales which follows will, in most respects, apply to all of the scales in the series.

Lewis and Dowding (51) and others have given us works on the anatomy and related phases of conifer bud morphology, but the best modern summary of the literature dealing with the general subject was given by Foster in 1928 (35). As early as 1880, however, Goebel (38) called attention to the shortening of leaves and of internodes during the

winter period of such scale-free conifers as *Auracaria* and *Juniperus* and pointed out the fact that, even within a genus, we may have some forms with bud scales and others without them, as in *Podocarpus*.

During the present work, the ontogeny of the scales was followed in *Pinus taeda* L., *P. palustris* Mill., *P. Laricio* var. *Austriaca* End., *P. sylvestris* L., and *P. Pinaster* Ait. The time of deposit and the time of extension were observed. Since the putting down of new units is a growth phenomenon, the deposit of primary foliar organs, when charted, gives the typical S-shaped curve of growth (Fig. 30). The extremes are marked by sterile scales, most of which are never separated widely from each other and are, therefore, termed bud scales. Since, however, the scales for a given year's growth are in two separated age groups, these are for convenience termed, in the order of their deposit, "Group A" and
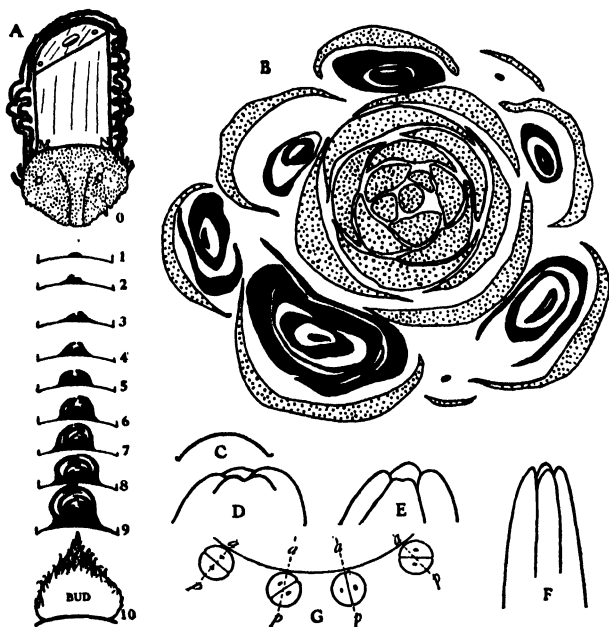
FIG. 7.—Miscellaneous.

A. Diagram of a longitudinal section of a two-needled dwarf shoot with normal interfoliar buds in various degrees of development.

B. Camera lucida tracing of a transverse section through the tip of a winter bud of *P. Laricio*. The black circles show the hooded nature of the scales on the lateral buds and fascicles.

C, D, E. F. Stages in the early development of cotyledons, showing reduction in number of primordia (after Buchholz).

G. Diagram of leaf orientation with reference to axial plane (*a, p*) in two-needled pines.

"Group B" (Fig. 2). Except for a difference in time sequence, the ontogeny of the bud scales is similar in the two groups. "Group A" on one year's deposit is in series proximally with "Group B" of the previous year and distally with the sterile bracts of the main axis. The outer scales in "Group A" become dry and frayed during their first growing season. The scale blades become dead and scarious in their outer portions but remain alive at their bases. A sharp line of demarcation sets off living tissue from dead tissue (Fig. 2 H). The scales in "Group B" spend the first winter as young tender scales or as meristematic primordia (Fig. 2 G). During the second growing season these follow through exactly the same ontogeny that has been described for "Group A."

FIG. 8.—Young bud scales of *P. pin-aster* showing the early stages of fraying.

FIG. 9.—Old scale from *P. pinaster* showing method of fraying and interlocked marginal fringes.

During the second summer while maturation processes are in progress, the origin of younger and more distal units (Fig. 1 K) slowly crowds the scales in "Group B" to the base of the developing bud, where they spend the second winter (Fig. 2 A). During the early spring of their third growing season the covering of bud scales is ruptured, and the scarious portions are either torn loose from the living base, as in the forms with deciduous bud scales, such as *P. sylvestris*, or remain attached as persistent bud scales, as in *P. palustris*.

The degree of bud scale specialization varies somewhat in the different species. The most elaborate specializations occur in species with long needles and persistent sheaths and are, therefore, well illustrated by *P.*
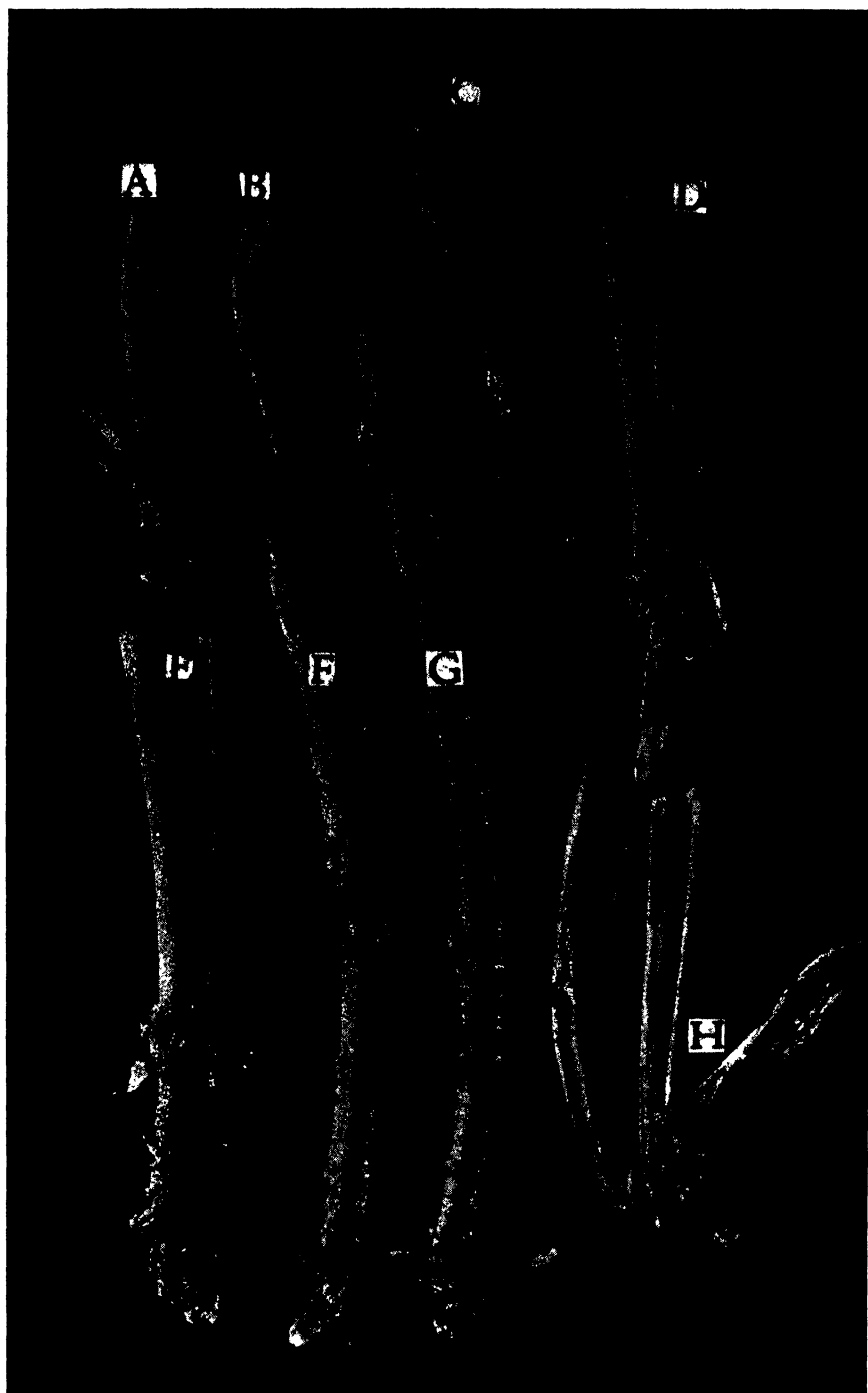
Fig. 10.—Fascicles and fascicle sheaths. (See explanation on opposite page.)

palustris (Fig. 6 D and E) and *P. Pinaster* (Figs. 8 and 9). Here the young bud scale, while still meristematic, forms a sort of hood (Fig. 11 B, C, and C') over the growing point of the stem and over all younger foliar structures. "Group A" passes these stages rapidly while "Group B" spends the first winter in the early stages of the process. Growth goes on at a more rapid rate in tissues on the margins of the hood. At this point the cellular orientation is such that, as the marginal cells elongate, a sharp angle is made with those of the scale blade (Figs. 8, 9, 11, and 12). As maturation proceeds, these marginal cells elongate enormously and become fibrous. The fibers are strong but are only loosely bound together laterally, so that, upon the deposit and expansion of the underlying structures, the resulting growth pressures rupture the older and more mature scales according to a predetermined plan. This is imposed by the nature and arrangement of the scale tissues and by the sequence of growth processes within the scale itself (Figs. 8 and 9). The angular arrangement and the fibrous nature of the tissues combine to bring about the splitting of the blade and the fraying of the overhanging hood-margin, especially along the line of angles where blade fibers and marginal fibers meet. These processes continue until the hooded condition is no longer recognizable, each separate structure having been transformed into a thin dry triangular scale with greatly frayed margin (Figs. 9 and 11 D). Upon the completion of these transformations the scale series form numerous superimposed layers of papery wrapping around the bud. The individual scales are interlocked by the tangle of tough marginal fibers, and, if loosened at their bases, they may be unrolled from the bud (Fig. 6 E) and still remain attached to each other. So tenaciously do they cling together that often a scale may be torn apart by simply pulling on the attached neighboring scales. When in position on the bud, considerable growth pressure is required to break these layers of binding material. For this reason the interlocked scales often form binding rings (Fig. 13 e) or caps (Fig. 13 f) on partly developed shoots.

The angular margins, frayed edges, and strengthening effect of the interlocking fibers were, in part, described by Lord Avebury (54), who, however, did not describe the manner of their production. Engelmann (30) and Pilger (70) also describe the delicate interwoven fringes at the

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Explanation of Fig. 10

A. Dwarf shoot of *P. cembroides* var. *monophylla* cut diagonally, with sheath in place at base of needle.
B. Same with sheath removed, pulvinus absent.
C. Dwarf shoot of *P. Cembra* after ·shedding of the sheath, pulvinus present.

D. Same with sheath in act of shedding.
E, F, G. Old, middle-aged, and young fascicles of *P. palustris*, showing progressive shortening of sheath by wrinkling.
H. Same as *D*.

margins of the scales. Dufrenoy (26) figures a fringed scale (similar to that shown in Fig. 11 D), and in describing his figure he says that the scale leaf is "strikingly similar to scale of Cycas; the hairs may be interpreted as sterilized ancestral ovules or stamens." The scale ontogeny proves the incorrectness of Dufrenoy's interpretation, for the fibers at the margins are neither hairs nor sterilized spore-bearing members but rather the frayed blade margins of foliar organs.

Nearly all investigators who have worked with the bud scales of pines are agreed that these scales exercise some sort of *binding effect* upon the
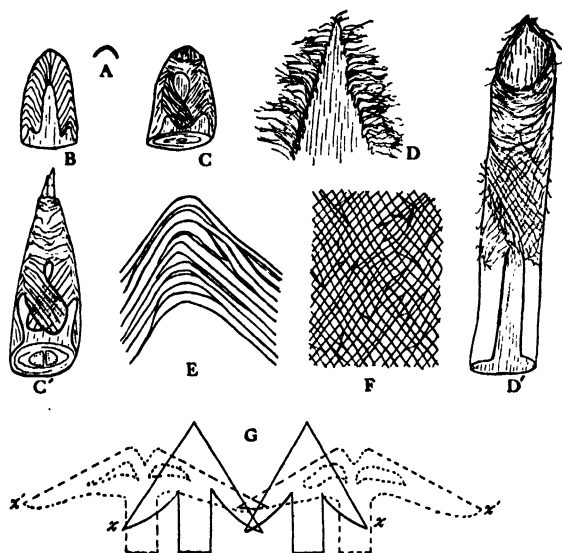
Fig. 11.—Stages in hooding, fraying, and perforation
of bud scales and sheath scales.

A. Young scale primordium.
B. Hooded young scale with angular marginal cells.
C and C'. Perforation of bud scales and sheath scales respectively.
D and D'. Mature bud scale and sheath scale respectively.

E. Cellular detail along marginal angle.
F. Detail of overlapping fibers.
G. Diagram showing how overlapping and angled margins permit expansion without disturbing the binding efficiency of bud scales.

tissues within. This fact should be borne in mind, for this binding phenomenon has probably had a part to play in leaf arrangement and in the progressive reduction of the leaf number on the dwarf shoots which, while young and plastic, are enclosed within the bud.

An exaggeration of the hooding phenomenon sometimes causes the underlying growing point to push out through the crown of the hood (Fig. 11 C and C'), and, as the underlying parts are lifted up, an en-

circling sheath of fibers is left behind (Fig. 11 D') after the manner of the orchrea in *Polygonum*. Hereafter this phenomenon is termed *perforation*.

The case of the scale on the long shoot is somewhat different, for, subsequent to perforation, an increase in diameter of the encircled stem soon ruptures the encircling fibers of the perforated scale. Perforated blades and encircling fibers, therefore, represent but temporary stages in
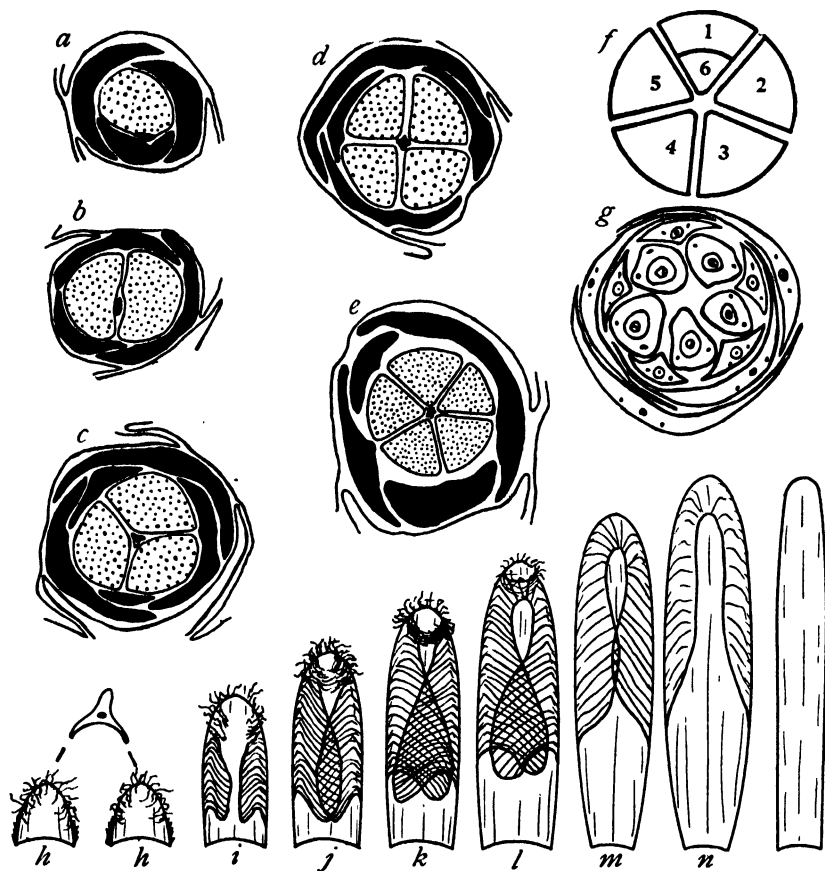
Fig. 12.—Needle shapes (and miscellany).

a, b, c, d, and e. Camera lucida tracings of transverse sections through fascicles having one to five needles, respectively.

f. Theoretical diagram of six-needled fascicle.

g. Outline of a section through a ten-needled dwarf shoot showing two whorls of five needles (after Schneider).

h to o. Semi-diagrammatic drawing of fascicle scale series at the time of perforation.

hh. Lateral scales.

i. Central scale with frayed margin.

j to l. Perforated scales.

m and n. Hooded scales.

bud scale ontogeny (Fig. 11 C and D). The insignificant increase in diameter of the dwarf shoot permits the perforated scales on it to remain as a more or less permanent encircling sheath (Fig. 11 C' and
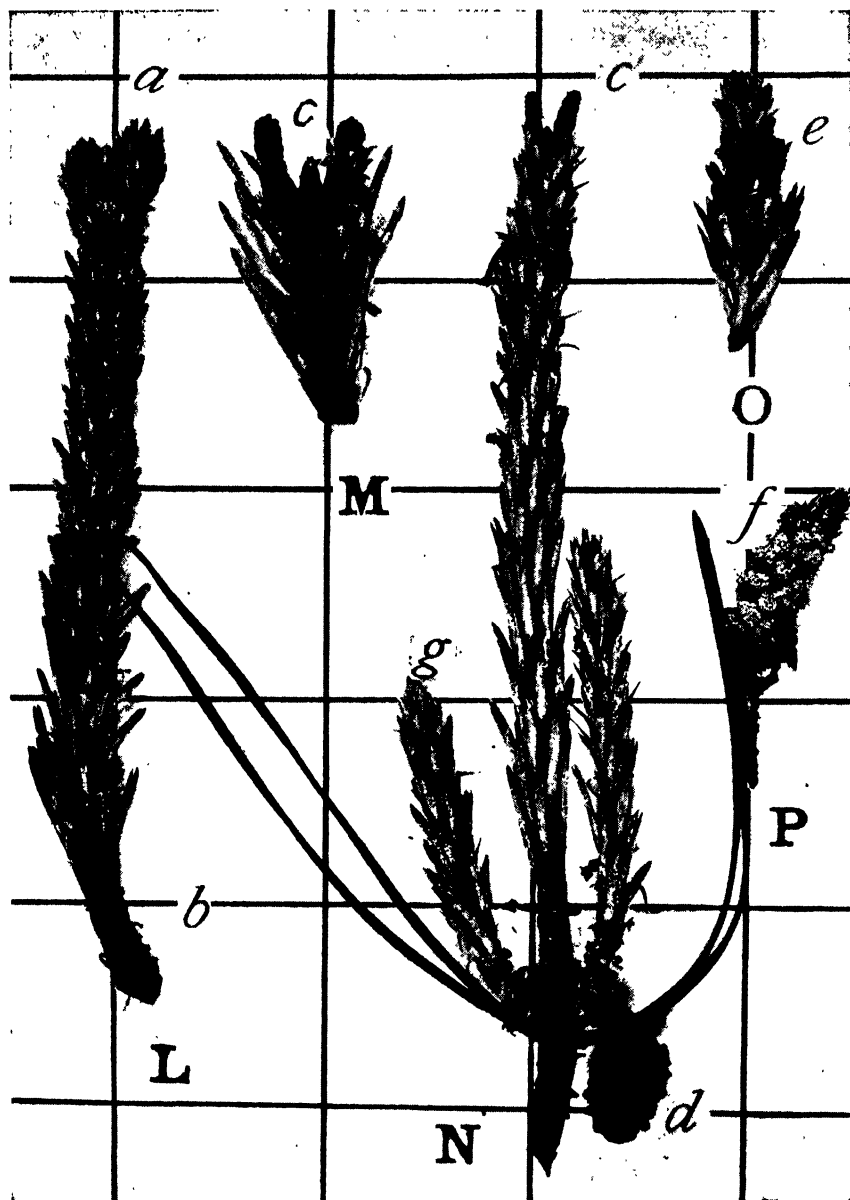
Fig. 13.—Young long shoots of *P. sylvestris.* (See explanation on opposite page.)

D') through which, by basal growth, the needles are forced as through a cylindrical die. As hinted by Eichler (29), it is this die-like action which gives the needles their characteristic cross-sectional forms (see Schneider, 79).

Except for a difference in the amount of extension undergone by the corresponding internodal components, the sterile bracts are in every way similar to the bud scales in "Group A" with which they are in direct series on the distal side.

On very vigorous shoots each year's growth usually has a number of units with extended internodal components but which are devoid of axillary buds (Fig. 13 b and Fig. 14 d to e). The sterile bracts or foliar components of these units lie between the last true bud scales and the first subtending bract. They usually remain in the bud for only a single winter. At extension of the main axis, the scarious portion is often lost and the living base alone remains. This remnant we may think of as a leaf scar or leaf cushion.

The line of demarcation between sterile bracts and the true bud scales is not a clearly defined one. After extension, the bud scales continue to occupy their crowded position at the base of the year's growth or, when shed, leave a ring of crowded scars to mark the points from which they have fallen (Fig. 3 m and n), thus dividing the twig into a series of easily recognizable annual growth segments (Fig. 15). The sterile bracts or bract scars do not remain crowded but at extension come to occupy relatively wide intervals along the base of the year's growth (Fig. 14 d to e), for at this time the two types of scales are similar and lie in continuous series at the base of the winter bud (Fig. 2 A and B). One cannot determine exactly what fractional part of the sterile scale series at the base of a dormant bud belongs to each of the two types. An approximation can be made, however, by counting the scars left on the same twig in previous years. This is made easy by the fact that most pines leave an indelible record of the various units produced on each year's growth long after their foliar components have disappeared (Fig. 3 E). In some cases the units produced in any given year can be counted with certainty

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Explanation of Fig. 13

L. Vigorous shoot with laterals.
    a. Lateral long shoots developing one season in advance of the usual time.
    b. Naked base covered with sterile bract scars.
M. Sectioned tip showing ovulate cones.
    c. Ovulate cones.

N. Long shoot with young and one-year cones and normal laterals.
    c'. Young ovulate cones.
    d. One-year ovulate cone.
    g. Normal lateral long shoot.
O. Branch with binding ring of bud scales.
    e. Binding ring.
P. Long shoot with staminate cones.
    f. Binding cap of scales.
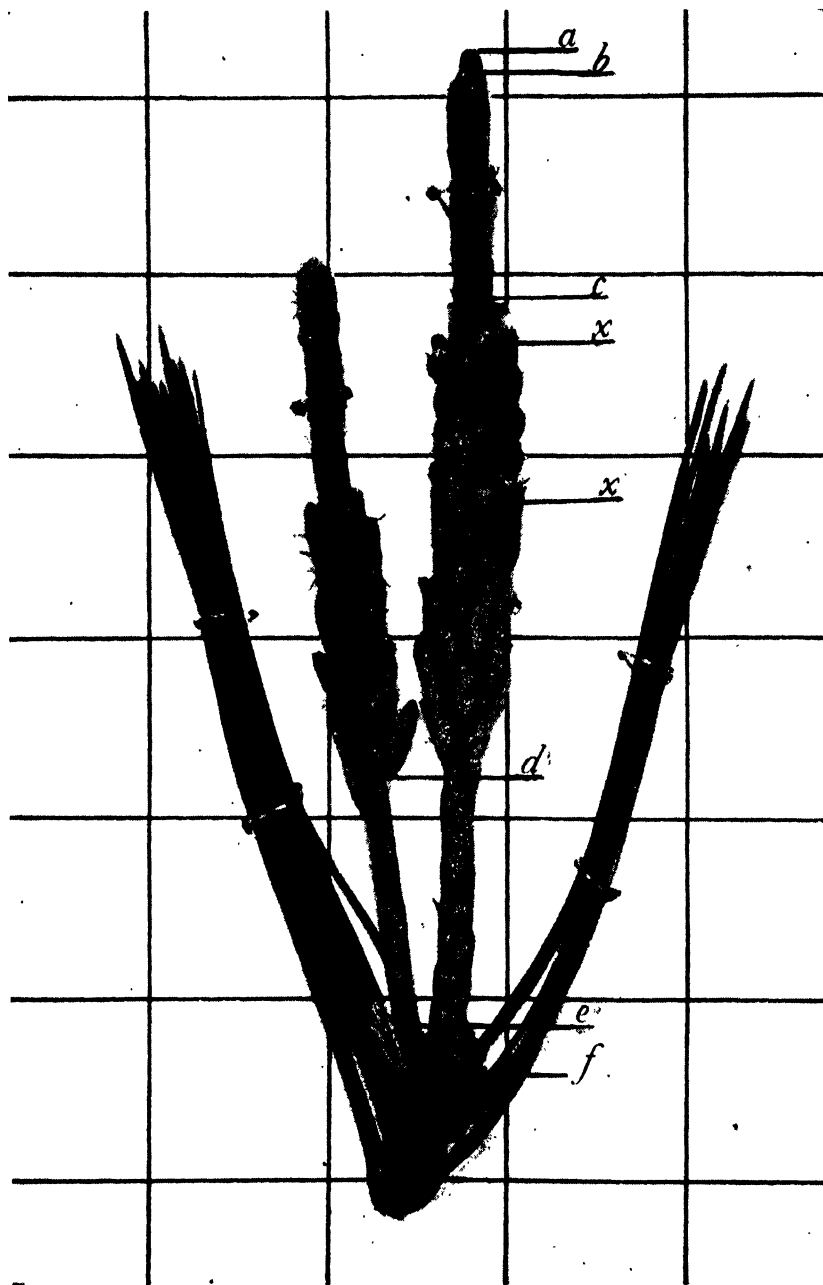
FIG. 14.—Young long shoots of *P. tonyosho:* The left branch is normal. The right branch has the staminate cone series interrupted by bisporangiate cones. (See explanation on opposite page.)

for periods in excess of a quarter of a century (Fig. 15). After the counts are made and averages taken, one may divide the total bud units in the sterile series of the dormant bud into two approximately correct groups, using for this purpose the average percentages of scales and of sterile bracts produced by the same twig in previous years.

At its distal end, the sterile bract series is continuous with the staminate cone series (Fig. 14); but if, as is often the case, the latter is omitted, then direct contact is made with the dwarf shoot series (Fig. 13 L and N). The first fertile scale in either orthostich or parastich usually marks the beginning of the fertile series, which, from that point to its end, remains unbroken. This is not always the case, however, for staminate cones may intrude themselves into the dwarf shoot series or vice versa.

A similar overlapping is found between sterile bracts and cones and also between sterile units and fascicled units. These interruptions are not always confined to the borderline between series. In *P. palustris*, and less frequently in other species, interruptions by the intrusion of one or several units of a different type occur well up in the body of a series. This is especially true of the intrusion of sterile units into the dwarf shoot series. Such gaps occur most frequently on the ventral surface of horizontal twigs (Fig. 16 A). Gaps in the various fertile series are especially frequent on those twigs on which the scale leaves have been replaced by simple leaves (Fig. 5).

The fertile units of a given year's growth, save for the presence of axillary outgrowths, are similar in every way to the extended sterile units described above; and the accompanying scales are in every detail like those already described.

Before leaving the general subject of scales, it is probably worth while to restate the chief points in regard to these organs. It seems certain that regardless of type the scales have developed from leaves of a simple nature. The main peculiarities of pine scales, in comparison with the scales of other plants, are bound up with the phenomena of hooding, fraying, and perforation, the results of which permit the scales to exert binding pressures upon the organs growing within them. *Pinus* is also peculiar in that all the primary foliar organs are normally scale-like.

<div align="center">Explanation of Fig. 14</div>

a to b. Normal ovulate cone.
b to c. Dwarf shoot series.
c to d. Staminate cone series.

xx. Bisporangiate cones in staminate cone series.
d to e. Sterile bract series.
f. Bud scale scar.
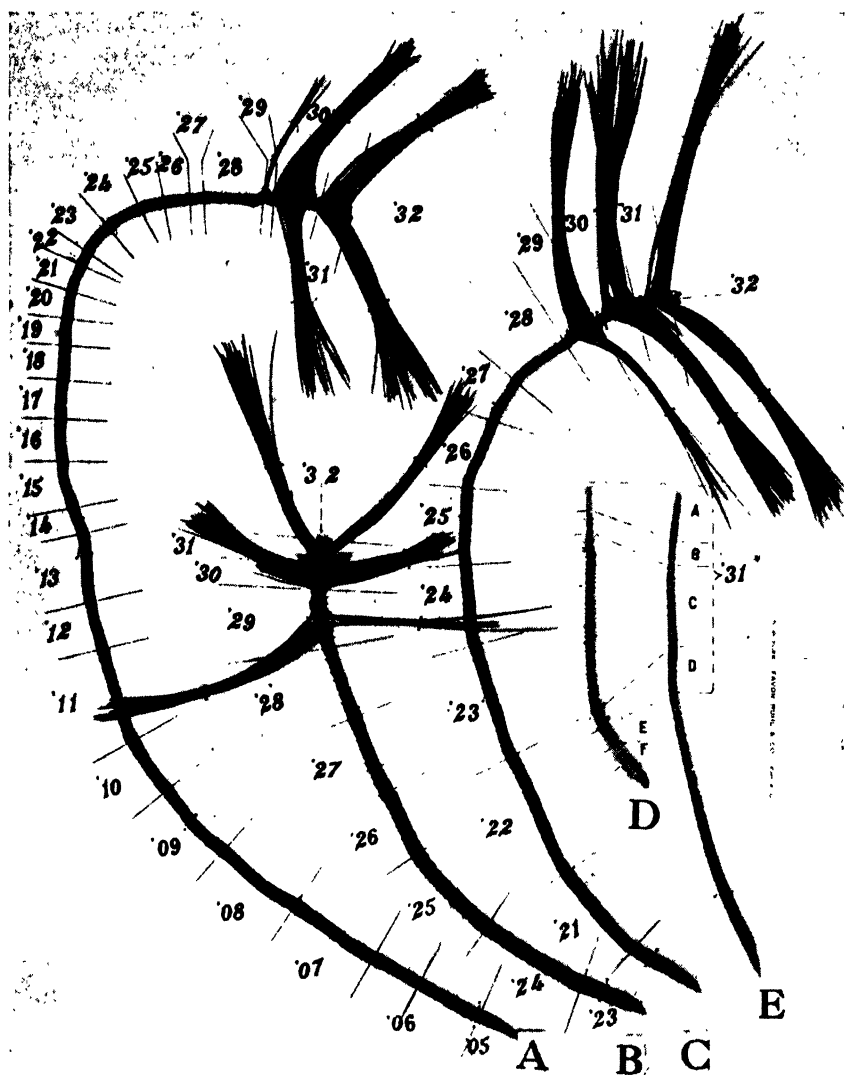
Fig. 15.—Twigs of *P. Laricio* from the north (Illinois) and of *P. palustris* from the south (Texas) with dated annual growth nodes.

A. Twig of *P. Laricio*, normal except for 1929, a year in which the terminal bud was destroyed. Subsequent growth came from a lateral bud.

B. Twig of *P. Laricio*, normal except for shortening of internodes and leaves of 1930 due to transplantation of the mature tree in the winter of 1929.

C. Normal twig of *P. Laricio*.

D and E. Stripped twigs of *P. palustris* showing multinodal growth for 1931.

C. Homologies of the Axillary Shoots

Turning now from the foliar to the axillary components on the vegetative long shoot, we find these to be of four types, viz., staminate cones, dwarf shoots, branch buds, and ovulate cones. The staminate cones and dwarf shoots fall naturally together in one group, and the branch buds and ovulate cones comprise another.

The staminate cones and dwarf shoots are alike in origin and in position. They have determinate growth and are deciduous. Each is clothed at the base with a series of thin scales. Without a clear borderline between them, the cone and dwarf shoot series lead directly into each other. These facts make it clear that in *Pinus* the axis of the staminate cone and that of the dwarf shoot are of the same order and are as nearly homologous as it is possible for fertile and vegetative shoots to be.

Near the end of a year's growth and terminating the orthostiches of fertile units on the long shoot, one to several branch buds occur. These usually deposit their basal scales during their first season (Fig. 2 E). The fertile units for their first year's growth are deposited during the second season, and extension of their first year's growth occurs during the third season (Fig. 13 g). On vigorous shoots this program can be shortened (Fig. 13 a), in which case the lateral long shoots are seen as lateral extensions of the year's growth upon which they are borne. In this position they are strikingly suggestive of young ovulate cones which not only occupy similar positions (Fig. 13 a and c) but originate at the same time in the ontogeny of the year's growth. The presence of secondary dwarf shoots (brachyblasts or seed scales) upon their axes mark the cones as modified long shoots, as does also the frequent proliferation of their growing points into long shoots. These evidences make it clear that the ovulate cones and the lateral long shoots are of the same order and that the ovulate cone, therefore, should be looked upon as a modified long shoot.

D. Normal Annual Growth of the Vegetative Long Shoot

Without attempting to analyze the complex of physiological conditions upon which the regular sequence of events within a pine bud is dependent, the story of seasonal bud behavior is briefly outlined below:

Upon the return of favorable growing temperatures following the winter rest, the internodal tissues of the bud units (Fig. 2) are first to spring into vigorous activity. Although the other parts (dwarf shoots, sheath scales, needles, etc.) seem ready to grow, something seems to inhibit them. Only the cones are able to compete with the internodal cells as the latter enter actively into their long delayed grand period.
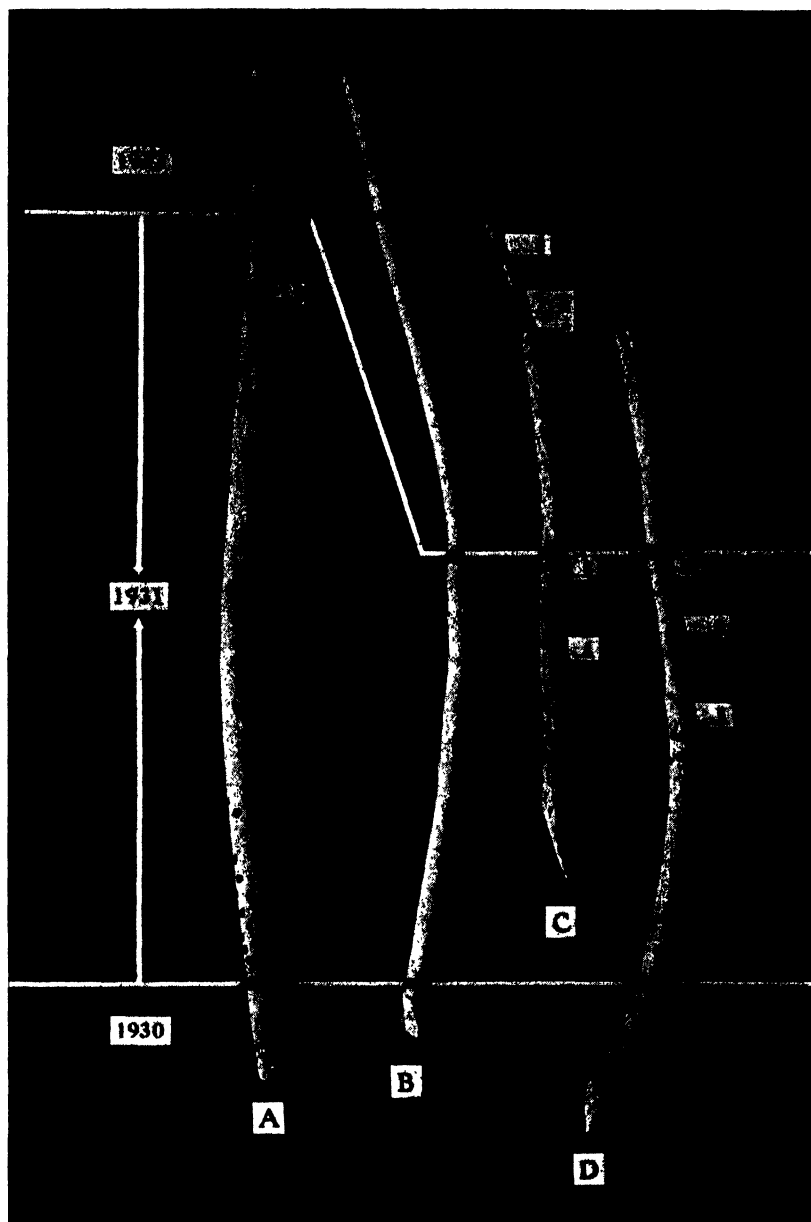
Fɪɢ. 16.—Stripped twigs showing annual growth nodes.

A. Ventral surface of a twig of *P. pa-lustris*. Inked circles show blanks in the dwarf shoot series. The series was continuous on the dorsal side.

B. Twig of a white pine from Massachusetts.

C and D. Multinodal twigs of *P. palustris* from Texas. The numbered segments represent successive fertile series deposited during the years indicated.

As the internodal tissues pass the crest of their grand period and begin maturation, the tissues of the dwarf shoots and of their foliar organs (sheath scales and needles) spring into vigorous activity. These, as pointed out by Küster (49), all spend the winter in approximately the same developmental stage. As the outermost scales of the sheath begin to mature, the needles in their turn become the conspicuous extension organs. Their growth is accelerated for a time, but, as the summer approaches, it becomes slower and more irregular.

Soon the distal portions of the scales and leaves become matured and growth becomes confined to narrow basal zones. While active growth is still in progress, the matured portions probably carry on their full share of photosynthetic and protective work respectively. While leaf, scale, and cambial growth are still active, the deposit of new units is begun at the growing point of the long shoot. This manifests itself first by a slow addition to the sterile primordia already present at the tip of the axis ("Group B" of previous season). As the growth processes become more rapid, fertile units are deposited (Fig. 1 K). On slowly growing twigs the fertile series usually begins with pollen cones followed by short shoots. The cones may, however, fail entirely. On vigorous twigs pollen cones are seldom deposited, and in this event the first units in the fertile series are dwarf shoots.

The time sequence for both deposit and extension is somewhat variable, depending upon the species, the latitude, and the season. The different species in a given locality start activity at approximately the same time and at first run parallel courses. As summer progresses, the species which mature their needles early (usually those with short needles) advance more rapidly and begin the deposit of new units, while the species with long needles are continuing the growth of these organs. As fall approaches, however, the species with long leaves and a proportionately greater photosynthetic area are accelerated in their processes; and, by the onset of the winter rest, all have attained corresponding growth stages.

E. Abnormal Annual Growth of the Long Shoot

1. Multinodal Annual Growth and Summer Shoots

In case the season of deposit is interrupted by a hot dry period followed later by rains and a return of favorable conditions, a so-called multinodal year's growth is produced. These multinodal shoots are especially frequent in southern pines and are more likely to occur in some species than in others. This behavior was observed most commonly in *P. palustris* growing at College Station, Texas. Indeed, multinodal growth in this case was more the rule than the exception (Fig. 16 A, C, and D).

It was found that by stripping the bark from a year's growth the separate series of fertile units could be displayed to good advantage. This is made possible by the fact that those portions of the wood from which sterile bracts are stripped appear smooth. The woody cylinders leading to the dwarf shoots, however, clearly mark the points from which these structures grew (Fig. 20 D and E).
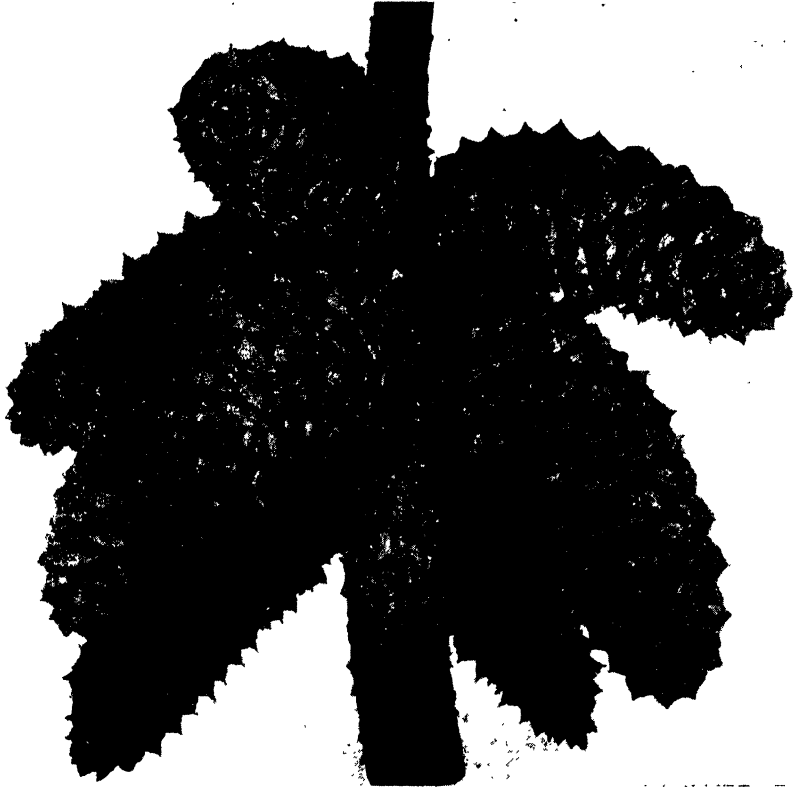
FIG. 17.—Two sets of mature cones of *P. taeda* produced in the same season as a result of multinodal growth.

In each case of multinodal growth, as conditions become unfavorable, the twig behaves exactly as if ceasing deposit for the year. The dwarf shoot series gives way to the usual number of lateral buds (and ovulate cones, if these are to be produced), after which the regular series of scales ("Group B") is deposited. When favorable conditions return, the dwarf shoot series is resumed and continued until again brought to a similar close. This process may be repeated a second or even a third time in a single summer (Fig. 16 C and D).

Multinodal shoots are related to the so-called summer shoots which sometimes result when the season is unusually long and the break between favorable seasons is marked. In this case the units which are deposited in the early period may be extended in the fall or late summer of the same year in which they were deposited. This occurred on many twigs of *P. palustris* and *P. pinaster* at College Station, Texas, in the summer of 1932.

2. Lateral Cones

If, as pointed out by Shaw (82), the multinodal twig under consideration is producing ovulate cones, those that close the first fertile series will be in the so-called lateral position, while those closing the last series will appear to be either terminal or sub-terminal. Actual terminal cones are extremely rare. Masters (57) says that they are never really terminal. Cases of actual terminal cones are on record, however, these having been described by Tubeuf (93) and Worsdell (104).

The production of two to several sets of cones on the same year's growth is common as shown by Mayer (59) and Gates (37). In the course of the present work numerous cases of this type were found, most of which occurred on trees from stations in Texas. Figure 17 shows such a specimen which produced, at the upper end of the first fertile series, a set of four cones and several branch buds. These were followed by numerous sterile scales and finally by a second series of dwarf shoots which again was terminated by four cones, making a total of eight, four of which were in the lateral position and four in the so-called terminal position. Each set of these cones occupied the same relative position with reference to a fertile series of units, the nature and order of which was determined by external conditions. As pointed out by Mayer (59), the so-called lateral cone, in the light of these observations, becomes a matter of ecologic interest rather than a fixed taxonomic character.

3. Intrusion of Ovulate Cones into Staminate Cone Series

Several young trees of *P. tonyosho* were observed in which ovulate cones had partly or completely replaced the staminate cones. These trees produced, in what ordinarily would have been the pollen cone series, staminate cones at the base, bisporangiate cones* in the middle, and ovulate cones at the top (Fig. 14 x). The plants which produced this curious arrangement grew as a border planting and had evidently been heavily fertilized. A somewhat similar grouping of cones has been reported by Fujii (36), who says that up to a certain stage the cones may

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*Of these cones more will be said in the section dealing with the seed scale, where their transitional scales will be discussed.
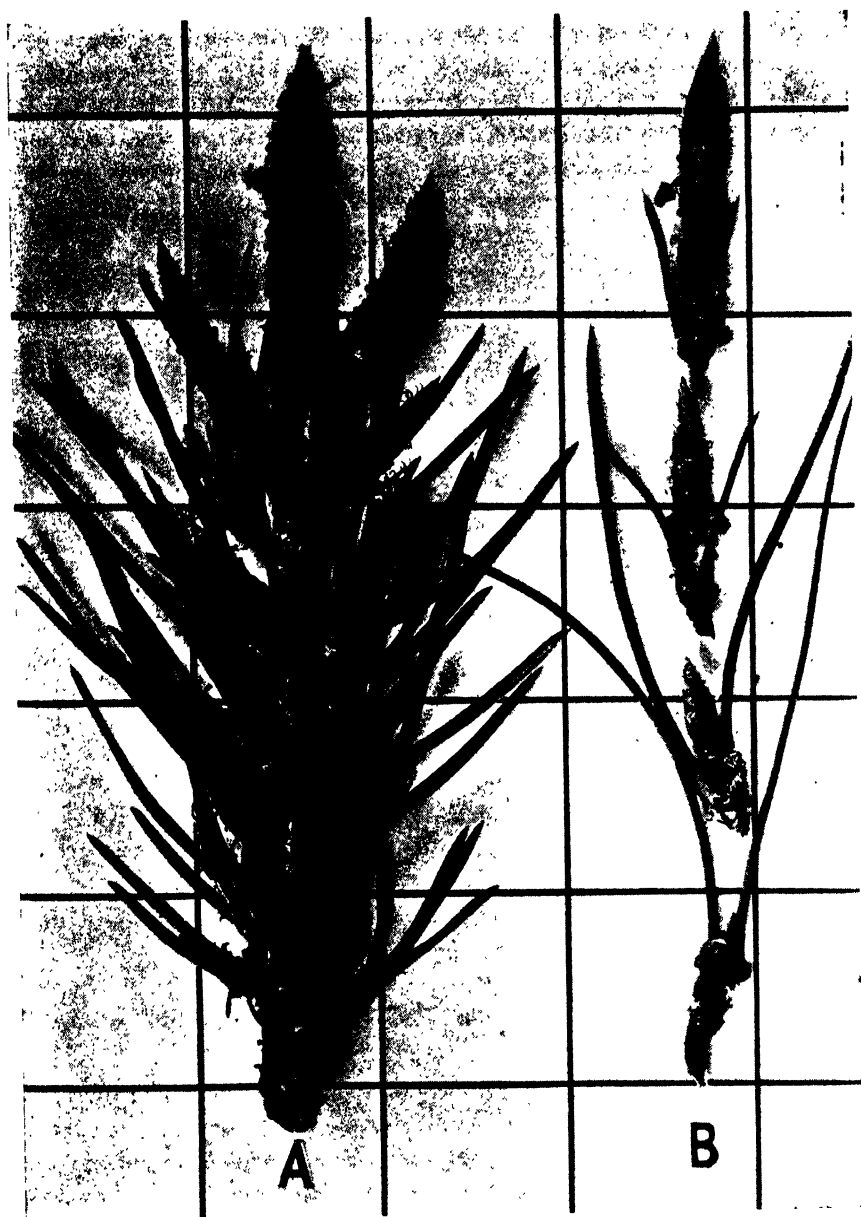
FIG. 18.—Abnormal long shoot and dwarf shoot of *P. pinaster*.

A. Long shoot with dwarf shoots in place.

B. Dwarf shoots from *A*, showing over-developed interfoliar buds and the relation of leaf length to bud size.

be developed into pollen or ovulate types, depending upon nutritional conditions. Similar bisporangiate cones have been reported by Righter (73) and by Meehan (60). The latter has even proposed a "law of sexuality" for the conifers, in which he holds that the "sex" is determined by the vigor of the twig upon which the cones are borne.

The replacement of other fertile units by ovulate cones expresses itself variously (Fig. 19 D). Sometimes the physiological condition is such that all the axillary outgrowths are replaced by ovulate cones. This condition has been reported by Keslercanek (48), Mullins (63), Witmack (103), Tubeuf (94), and others. As many as ninety-six ovulate cones have been found in series on a single twig.

4. Abnormal Axillary Bud Development

Another case of abnormal annual growth involved several twigs of *P. pinaster* growing at College Station, Texas. For some reason the growth of dwarf shoots on these did not stop at the customary point but proceeded in each case to make a long dormant bud (Fig. 18). Since these abnormal short shoots were borne at all axils, the long shoot, although little modified, may be looked upon as being abnormal in its secondary product. A similar twig has been reported for *Abies* by Tubeuf (94), who states that they are of frequent occurrence in this genus. This observation is interesting in that it is suggestive of a latent ability of *Abies* to produce branches in the axils of all its leaves. This suggestion is further strengthened by the fact that members of this genus often produce dwarf shoots as shown by Masters (57), or proliferate the seed scales into shoots as shown by Stenzel (86) and others.

III. THE REPRODUCTIVE LONG SHOOT, OR OVULATE CONE AXIS

A. Primary Foliar Organs

Near the point of attachment to the main axis, the ovulate cone produces several sterile units which bear scale-like foliar components, or involucral bracts (Fig. 1 H^2). Morphologically these are very similar to the scales already described for the main axis. They are broader, however, less frayed at the margins, and are probably never perforated.

Higher up on the cone, fertile units are borne. The axillary component of each fertile unit is the much-discussed seminiferous scale. The primary foliar component of these fertile units is the cover scale (Fig. 1 C^5). In the pines it remains small and woody and is sometimes partly fused against the seed scale. That these structures are indeed leaves,
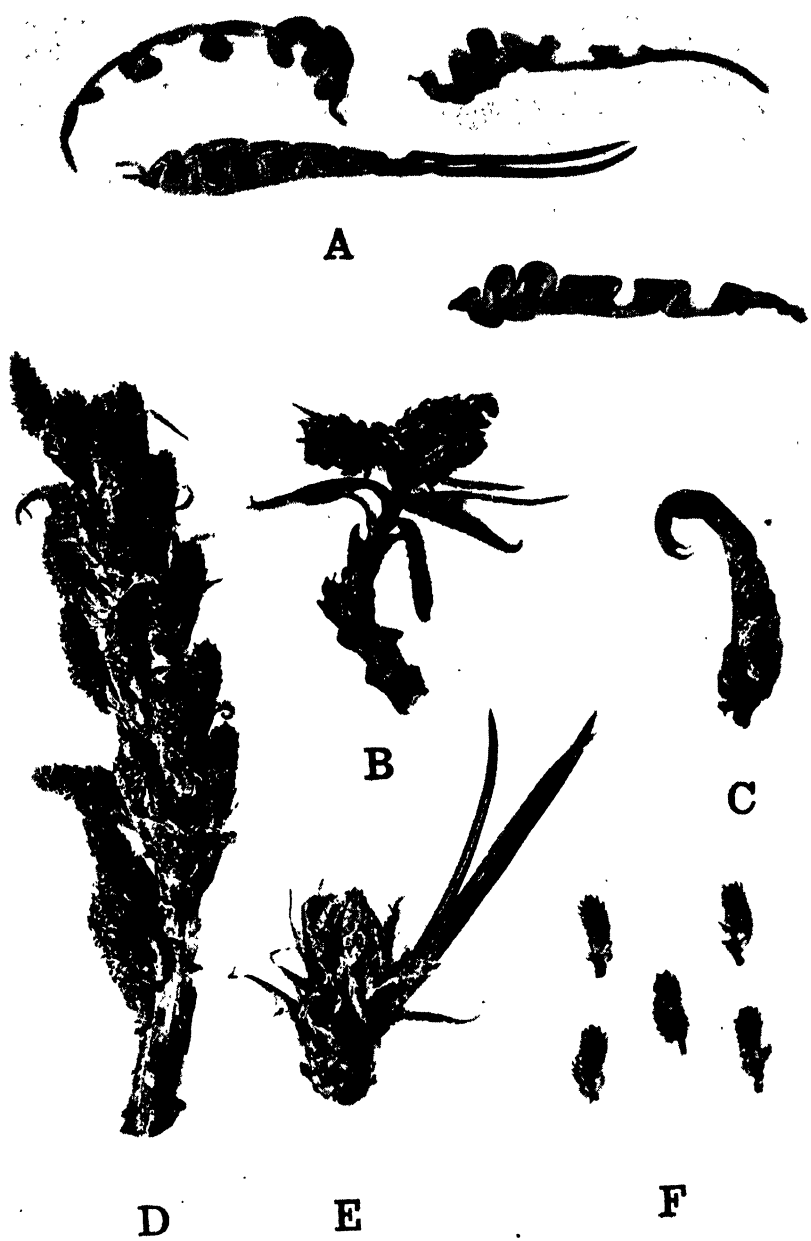
Fɪɢ. 19.—Miscellaneous. (See explanation on opposite page.)

at least in *Abies,* has been shown by Willkomm (102). In *Larix,* as was pointed out by Masters, they grow into functional leaves (Fig. 24 G).

As shown by Aase (1), the vascular strands from the cone axis to the bract and seed scale vary somewhat, depending upon whether one examines the tip, the middle, or the base of the cone. The middle or functional region tends, however, to give off bundles to bract and seed scale exactly as the vegetative long shoot gives off bundles to the subtending scale and the short shoot (Fig. 23 A and J).

B. Growing Point

On the cone axis the tip meristem usually is transformed entirely into woody vestiges which give no evidence of an earlier latent ability to continue into foliage-bearing branches. However, as shown by Masters (57), Thiselton (89), Stenzel (86), Willkomm (102), Tubeuf (95), and others, and as I have observed in several relatives of *Pinus,* indeterminate growth of the cone axis is not uncommon. Masters (55) and others have described proliferated cones in *Larix,* a genus in which these cones seem to occur most frequently. During the present work several such cones were found growing on *Larix europea* at Urbana, Illinois. Coulter and Chamberlain (22, p. 414) express the opinion that certain gymnosperms, like *Torreya,* have evolved beyond the stage of the compound strobilus by simply proliferating the cone axes and then transforming all the scales, save one, into leafy shoots.

Certain proliferated cones of *Abies* which were described by Willkomm (102) so closely resembled the precociously proliferated branch of *Pinus pinaster* (Fig. 18) described above, that for comparative purposes a few of Willkomm's figures are here reproduced (Fig. 29 z and z'; Fig. 32, parts 7, 8, and 9). A comparison of these figures will reveal the fact that the subtending scale of the pine shoot has its counterpart in the leaf-like cover scale on the *Abies* twig. The lateral scales on the dwarf shoot of the pine twig (Fig. 25 C) correspond in position to the leaf-like lateral expansions (megasporophylls) on the secondary shoots of the proliferated *Abies* cone. The tip buds of the two are, of course, homologous; and no doubt the fascicle sheath scales and needles which

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Explanation of Fig. 19

A and C. Needles from bound fascicles of *P. palustris.*

B. Abnormal shoot of *P. pinaster* with simple leaves and staminate cones.

D. Staminate cone series of *P. tonyosho* largely replaced by ovulate cones.

E. Bud of *P. Laricio* with one fascicle developing one season in advance of its normal time.

F. Bisporangiate cones of *P. tonyosho.*
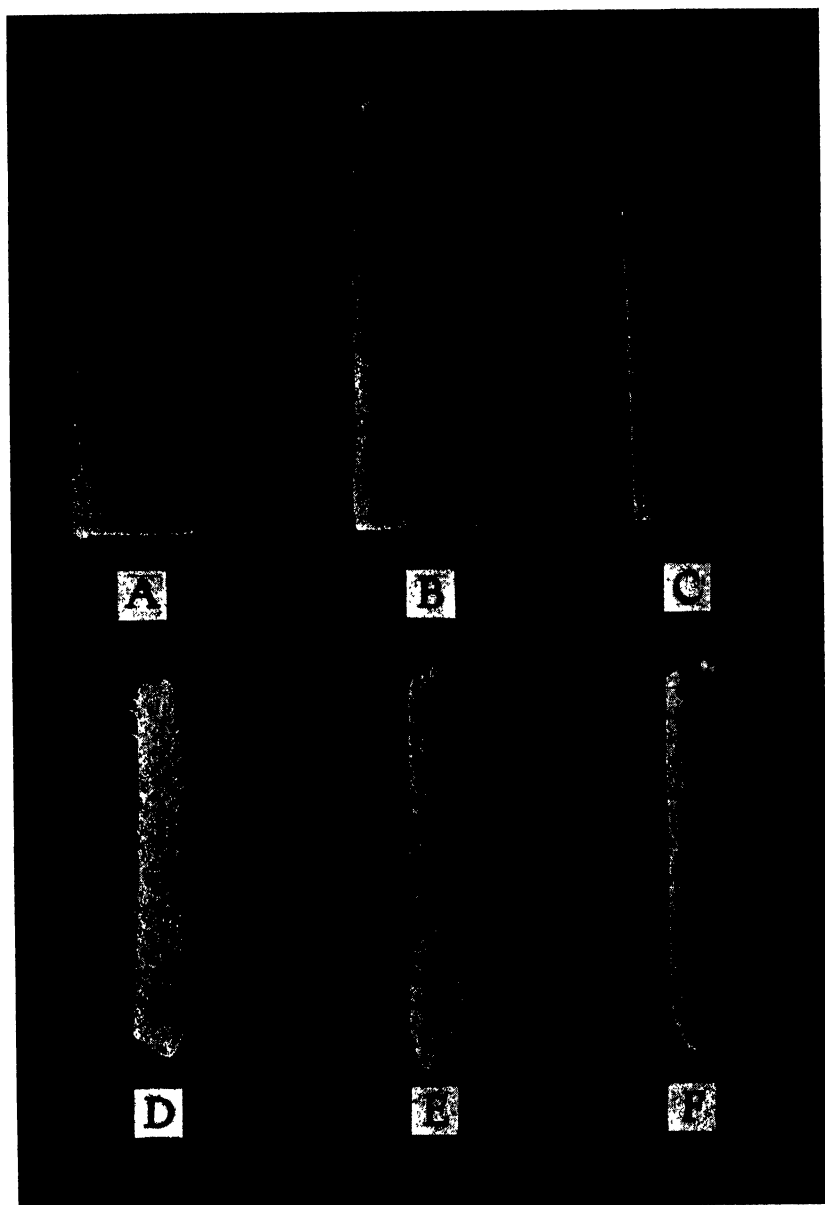
Fig. 20.—Comparative studies of the woody cylinders
of *Taxodium distichum* and *Pinus palustris*.

A. Stripped twig of *Taxodium* show-
   ing the projecting ends of
   branched dwarf shoots.
B. Same with surface layers removed.
C. Same in radial section.

D. Stripped twig of *Pinus* with the
   woody cylinders of the dwarf
   shoots projecting.
E. Same but older.
F. Same in radial section.

cover the bud in *Pinus* find their counterparts in the basal scales which cover the bud of *Abies*.

When it is remembered that the abietineous cone is a conservative structure and that the pine twig just described is only an exaggerated phase of a condition which occurs normally in this genus, one is impressed with the probability that some ancestor of *Abies* had dwarf shoots and that the present form of the genus has been attained by secondary loss of these structures. This view is further strengthened by the observations of Tubeuf (94) who found occasional vegetative twigs of *Abies* with buds in the axils of all their leaves.
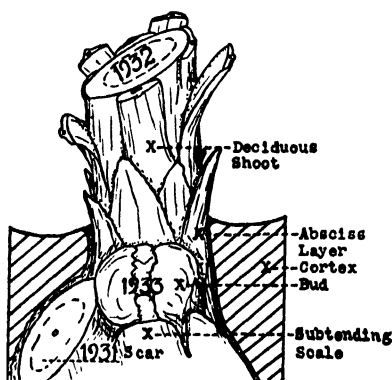
Fig. 21.—Diagrammatic drawing of the imbedded dwarf shoot of *Taxodium distichum*, showing the relation to successive deciduous shoots.

The tip meristem of another cone described by Willkomm had proliferated a long branch of ordinary vegetative type, the lower one-third of which had produced some axillary tissues corresponding in position and texture to the seed scales with which they were in series. These tissues filled up the space between the subtending leaf and the main axis, thus making the base of the latter concrescent (Fig. 29 x and x'). Since the seed scale is a dwarf shoot, this evidence suggests the possibility that the origin of concrescent leaves in conifers was associated with the disappearance of dwarf shoots from their axils.

In summary it may be said that exceptions to the rule of determinate growth of cones occur with sufficient frequence to convince us of their latent power of becoming indeterminate. The nature of these exceptions shows clearly that the megasporangiate strobilus is a compound structure and, therefore, its axis is equivalent to a long shoot and its scales are equivalent to dwarf shoots.

IV. THE EVOLUTION OF THE LONG SHOOT

A. The Vegetative Long Shoot and Its Foliar Organs

If we may assume that some remote macrophyllous ancestor of *Pinus* was devoid of resting buds and had both monomorphic branches and monomorphic leaves with no delay between deposit and extension (Fig. 29 a), then the steps in the evolution of the long shoot of *Pinus* with its characteristic, scale-like, primary leaves, its compound bud, and its well-marked annular growth-nodes, would seem to have been as follows:

1. Adaptation to temperate climates with seasonal climatic changes required protection of the meristematic tips. The plant met this need by a delay in the onset of the grand period of growth, thus bringing more and more foliar organs to overlap and protect the growing point.

2. The recurring need for protection during certain seasons (winter or drought) alternated with seasons of active vegetative growth and thus tended to fix the protective function on certain of the leaves on the long axis. These became specialized in this work and were transformed into scales. The remaining leaves on the long axis remained crowded within the scaly cover during unfavorable conditions and were later extended as food makers. The scales with their protected content of embryonic units thus formed a simple bud (Fig. 29 c and d).

3. A still further delay, both in the time of deposit of units of the main axis and the time of extension, led to a further telescoping of parts until all the primary leaves became scale-like; and the rudiments for the lateral units were produced before leaving the bud, thus leading to the formation of the *compound bud* (Fig. 2) which limited and shaped the growth of the enclosed short shoots.

4. The periodic extension of the compound buds gave rise to the characteristic annual growth nodes of the long shoot (Fig. 15) as already described.

B. The Ovulate Long Shoot, or Cone Axis

That the steps leading to the compound ovulate strobilus closely paralleled those leading to the formation of the compound winter bud is attested, first, by similar vascular units (Figs. 23 A and H) and, secondly, by the same arguments which were used earlier in this paper to support the homology of lateral long shoots and ovulate cone axes. The cogent fact that their secondary outgrowths (dwarf shoots and cone scales) run such close parallels is also suggestive of a parallel in the evolution of the long shoot and the cone axis.

The steps leading to the compound strobilus were taken at a time when the ancestors of *Pinus* were perhaps at the Cordaitean level. So re-

mote was that period that little fossil evidence of the course of this evolution has as yet been found. If the supposed parallel between vegetative and fertile long shoots is an actual one, then the compound strobilus must have resulted from internodal shortening of a fertile long shoot which bore numerous simple fertile shoots at its nodes. In a manner analogous to that by which numerous dwarf shoots were brought together to form the compound bud, this shortening brought together the numerous simple strobili, or primitive seed scales (Fig. 32, parts 1, 2, and 3) into a compound strobilus. Just as pressures within the compound bud *limited, shaped,* and *displaced* the sheath scales of the dwarf shoot, so the formation of the compound strobilus *limited, shaped,* and *displaced* the sporophylls on the simple strobili.

V. THE VEGETATIVE DWARF SHOOT AND ITS FOLIAR ORGANS

Turning now from the cone and the more or less generalized long shoot to a consideration of the shortened and highly specialized dwarf shoot, we find that its primordium is put down in the axil of the scale
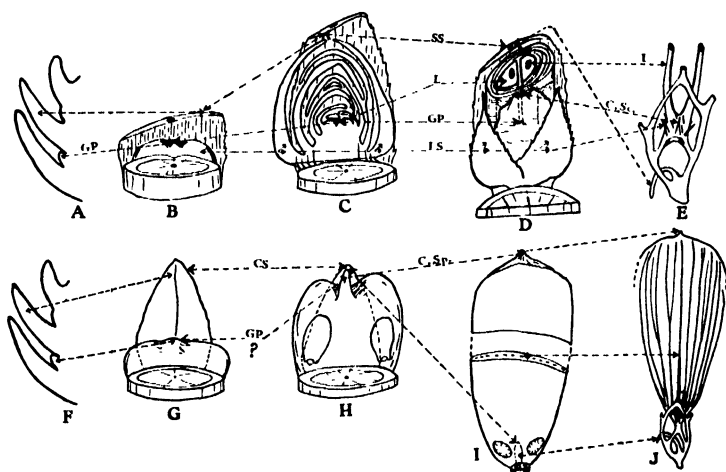
FIG. 22.—Diagrams showing corresponding structures as they appear during the development of the dwarf shoot and seed scale of *Pinus*.

A to E. Stages in the development of the dwarf shoot and its vascular supply.
F to J. Corresponding stages in the development of the seed scale.

SS. Subtending scale.	CS. Cover scale.
GP. Growing point.	CSc. Central scale.
L. Leaf.	CSp. Central sporophyll.
LS. Lateral scale.	
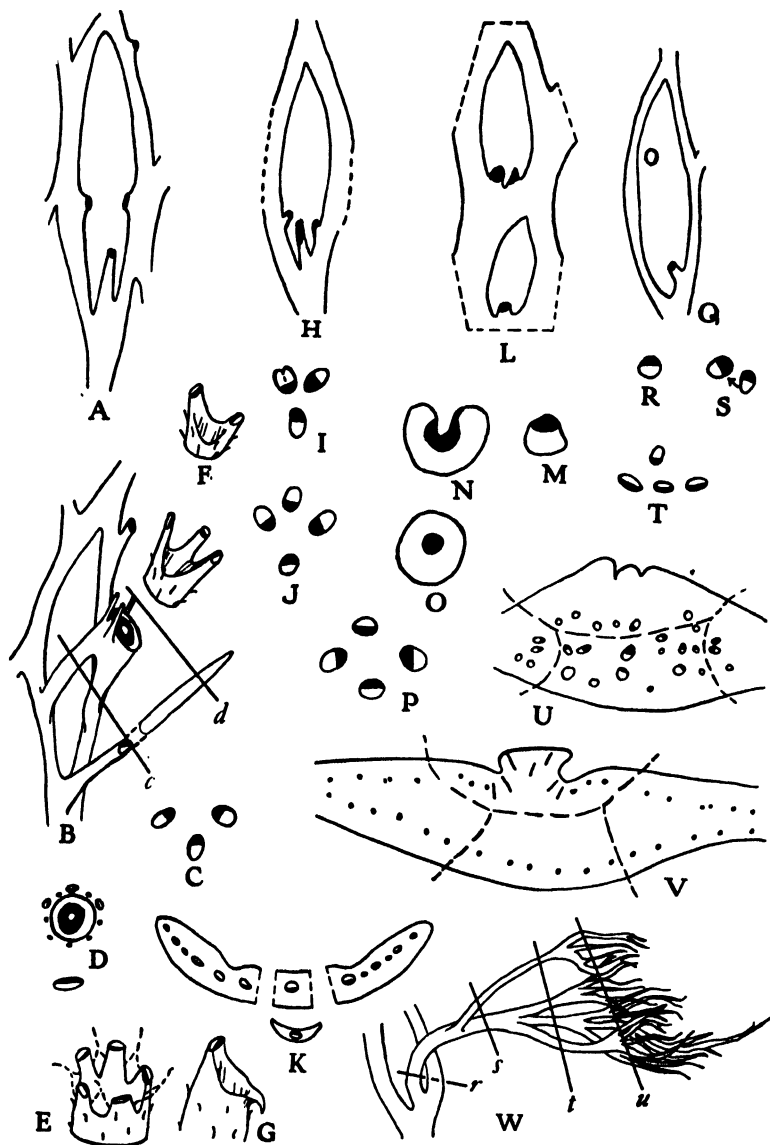
FIG. 23.—Diagrams of vascular structures showing the writer's views with reference to the relationships existing between the dwarf shoot of *Pinus,* the cone scale of *Pinus,* and the cone scale of *Araucaria.*

A. Supply to dwarf shoot and subtending scale of *P. Banksiana* (redrawn from Aase).

B. Same as *A,* but with supply to sheath scales and needles added.

C and D. Transverse sections through vascular supply to three-needled dwarf shoot. The bundles to the lateral scales and the central scale are exaggerated for emphasis.

primordium in mid-summer (Fig. 1 K and Fig. 30). The young dwarf shoot primordium gains rapidly the rudiments for all its sheath scales and for its functional leaves as was shown earlier. All these structures are extended during the season following their deposit.

A. SHEATH SCALES

1. Morphology

In all pines examined, the three most proximal of the foliar organs on the dwarf shoot were regularly and definitely placed with reference to the axes of both the long and dwarf shoots. The first two were always on opposite sides of a plane passed through the long axes of both the dwarf shoot and the long shoot (Fig. 1 N and Fig. 25 C), and the third was directly between the two axes and was bisected by their common plane. Hereafter in this paper this plane will be spoken of as the *axial plane;* the first two scales on the dwarf shoot will be called the *lateral scales;* the third scale will be termed the *central scale.*

The lateral scales are opposite each other, thickened at the base, keeled, and exhibit little or no intercalary growth. They are seldom perforated but are often serrate on the keel, and in other characters they are set off sharply from the papery sheath scales which follow them (Fig. 22 D and Fig. 12 hh).

Granting that the two lateral scales represent successive foliar organs on the dwarf shoot, it follows that the internode between them has been lost and that the scales have been displaced from their phyllotaxic positions. This view is supported by the fact that if we begin far enough

Explanation of Fig. 23 (*Continued*)

E. Supply to five-needled fascicle showing in dashed lines the location of the supply to the inner circle needles when present (drawn from Schneider's description).

F. Supply to two-needled fascicle.

G. Supply to the one-needled fascicle showing vestige of bundle to the aborted leaf as found in *monophylla* (from Schneider's description).

H. Supply to typical cone scale and bract (modified from Aase's drawing of *P. maritima*).

I and J. Transverse sections through H at different levels (redrawn from Aase).

K. Diagram of final distribution of the four bundles seen in *J.*

L. Diagram of supply to lowest scales and bracts on typical cones of *Pinus* (redrawn from Aase's figure of *P. Banksiana*).

M, N, O, and P. (Redrawn from Aase's figures of *P. Banksiana*).

Q, R, and S. Supply to scale of *Araucaria Balansi* (modified from Aase).

T. Diagram of principal bundles in scale of *Araucaria.*

U. Subdivision of bundles in sterile scale of *A. Balansi* (modified from Aase; dashed lines separating branches of principal bundles supplied from her description).

V. Diagram of a cross section of *Agathis vitiensis* (modified from Eames).

W. Diagram of ramifications of bundles in scale of *Araucaria.*
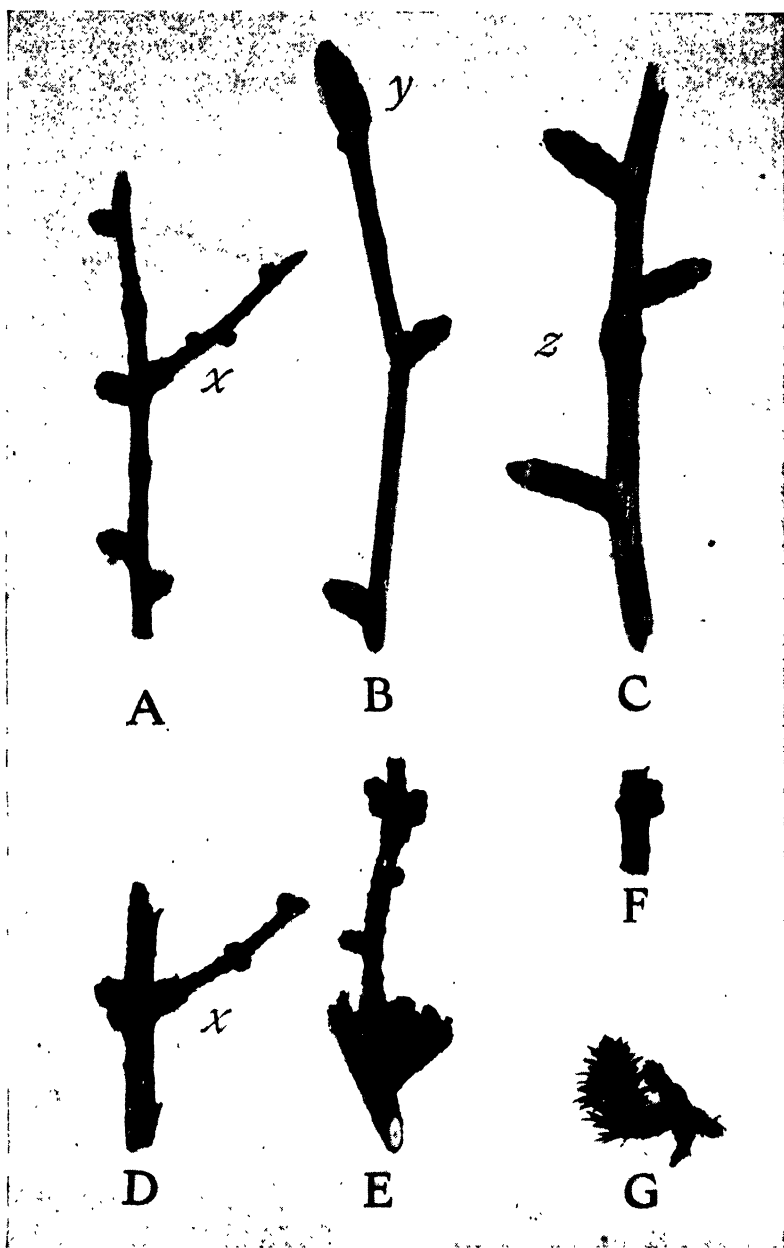
FIG. 24.—Dwarf shoots of *Larix* and *Ginkgo*.
(See explanation on opposite page.)

distally on the dwarf shoot, the angle between successive foliar organs regularly conforms to a two-fifths phyllotaxy; but, as the lateral scales are approached, the displacement becomes evident (see arrows in Fig. 25 C).

The central scale is displaced to a less degree and more closely resembles in form and texture the regular sheath scales. The differences separating it from the other scales would perhaps not justify the assignment of a special name to it, but, as will be shown later, the central scale has had a homologue in the evolution of the sporophylls to form the cone scale and demands, therefore, both a special name and special notice.

In addition to the lateral scales and the central scale, there is deposited on the young dwarf shoot a series of scale primordia which show little or no displacement. These are the regular fascicle sheath scales.

All the scales spend the winter in the meristematic condition (Fig. 25 F).

Spring growth (extension) begins almost simultaneously in all of these young scales, but maturation is in acropetal succession. This results in a constantly increasing length of scale from the proximal to the distal end of the fascicle scale series (Fig. 12 h to o).

In their later ontogeny, the scales follow through the processes of hooding, fraying, and perforation as described for the bud scales earlier in this paper. Here, however, these processes, especially perforation and the reverse growth of the marginal cells, are far more pronounced than in the bud scales already described. The situation is complicated still further by the development of intercalary meristems at the bases of the sheath scales by which these continue growth after perforation has been accomplished. Because the dwarf shoot undergoes such limited secondary increase in thickness, the sheath ordinarily encircles the base of the needles from which the scales may be slipped off one by one without being split.

With several superimposed layers of papery scales overlapping them and hindering their elongation, it is not surprising that pine leaves have developed needle-like points for perforating these layers. There is obviously a close correlation between the complexity of the sheath and the

Explanation of Fig. 24

A. Twig of *Larix europea*.
    x. A dwarf shoot which later extended to make a long shoot.
B. Long shoot of *Ginkgo*.
    y. A portion of the long shoot failed to extend, thereby making a dwarf shoot.

C. Normal *Ginkgo* twig showing wide interval between successive dwarf shoots.
    z. Bud scale scar.
D. Same as *A*.
E and F. *Larix* twigs with repeatedly branched dwarf shoots.
G. *Larix* cone growing from one member of a four-parted dwarf shoot.
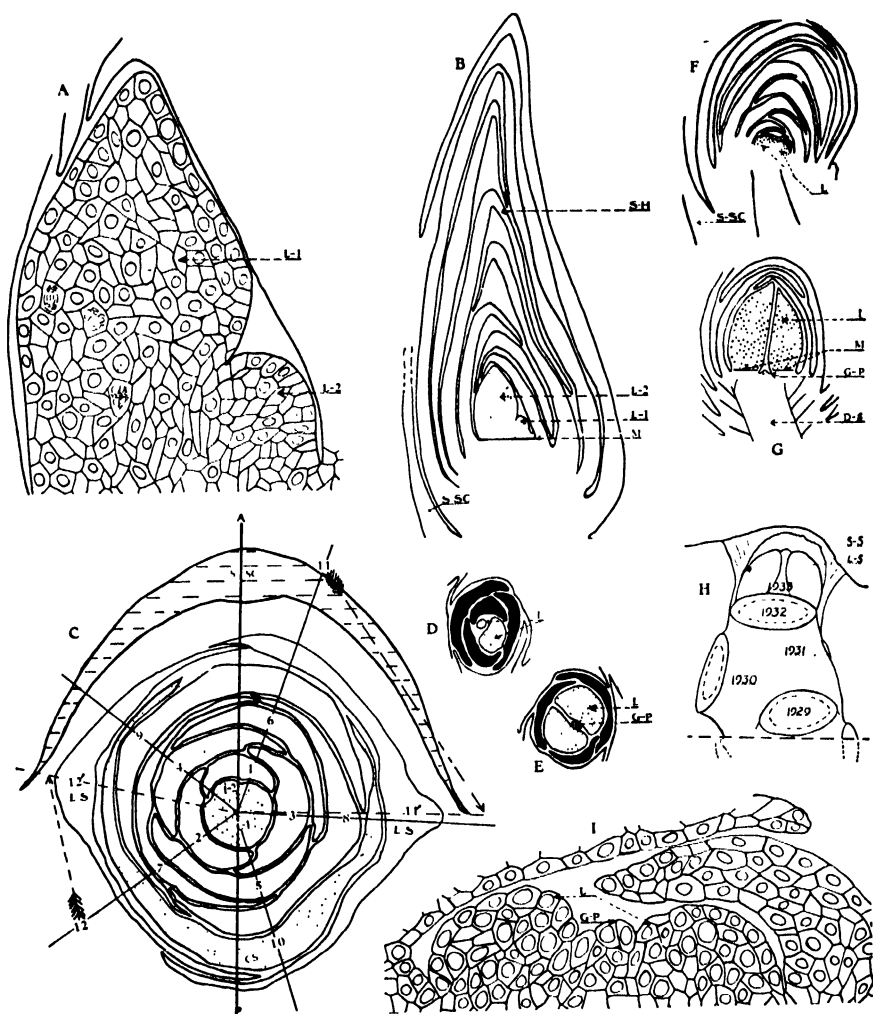
FIG. 25.—Comparative studies of the early development of leaves
in *P. cembroides* var. *monophylla* and *P. Laricio.*

A. Camera lucida drawing of a longitudinal section of the leaves of *P. cembroides*
var. *monophylla* soon after the beginning of spring growth.

B. The same less highly magnified and showing the hooded scales and other related
structures.

C. Camera lucida tracing of a transverse section through the developing fascicle
of *P. cembroides* var. *monophylla* showing the rudimentary second leaf, the
phyllotaxy, and the displacement of the lateral scales.

D and E. Cross sections of dwarf shoots from *P. cembroides* var. *monophylla* and
P. Laricio at stages corresponding to *B* and *F*, respectively.

F. Longitudinal section of winter dwarf shoot of *monophylla.*

G. Longitudinal section through young leaves of *P. Laricio* in a stage of develop-
ment comparable to that shown for *monophylla* in *B.*

H. Diagram of imbedded winter bud of *Taxodium distichum.*

I. Double leaf primordia of *P. cembroides* var. *monophylla* in winter condition.

development of horny and otherwise highly specialized points on the needles of *Pinus*.

Meehan (61) speaks of a "membrane" on *P. monophylla* which he says is present at the beginning of needle growth. By releasing this membrane Meehan thought that he could influence the number of needles on the dwarf shoot. Without doubt the structure referred to was nothing more than the multiple cover of sheath scales.

Collectively, the scales form a binding sheath for the fascicle of leaves. By reenforcing the point made weak by the basal meristems, the sheath makes possible the long-continued growth of the needles. In this respect the fascicle sheath is analogous to the encircling leaf sheath of the grasses.

The effectiveness of the sheath as a strengthening splint may be easily demonstrated by simply removing it from fascicles on which the leaves are actively growing. In this case the leaves fall limp, hang in a pendulous fashion, become dried at the base, and soon break off. The drying gives evidence of a secondary function of the sheath, i.e., the prevention of excess evaporation from the young parts which are as yet unprotected by a cuticle.

Once the needles are mature, the zonal meristems are lost. Mechanical and epidermal tissues are formed for parts within the sheath, and consequently its strengthening function is no longer required. This is evidenced by the fact that in many pines the sheaths are deciduous, falling away at the maturation of the leaf bases or soon afterward. Indeed the fascicle sheath, by obstructing the light from the basal portion of the leaf, becomes positively detrimental in that it appreciably reduces the photosynthetic area of the leaves.

2. Methods of Scale Removal

Pines have evolved several mechanisms for removing this obstruction. In some species the fascicle scales are more or less stiff and are weakly attached at their bases and have only a few of their distal scales perforated. As long as the needles are growing rapidly, the tissues within the encircling fibers are in the first phase of growth. The cells of such tissues are small, and consequently the total diameter of the encircled leaves is small. As elongation slows down and the maturation zone reaches points nearer and nearer the base, there comes a time when the enlarging basal portions of the leaves expand within the encircling fibers until the jacketing sheath is broken apart. Near the basal point of attachment an absciss layer is now formed from which the scales are soon broken by the movement of the leaves in the wind. The scales leave a bulging cushion or scar at points from which they fall away. When the

scales have been shed, the needles are left exposed to the light and air for their full length.

In *P. excelsa, P. flexlis,* and many others the scales are stiff and weakly attached at the base as described above, but the few perforated scales are more or less proximal in position. In this case the functional leaves, when mature, develop a special basal enlargement (Fig. 10 C and Fig. 1 L and M) which breaks the encircling fibers. The expansion of these structures forces the scales sharply outward and breaks them off, leaving the mature dwarf shoot entirely free of scales (Fig. 10 D, H, and C).

A third method of ridding the fascicle of its scaly sheath is found in *P. cembroides* in which the scales and leaves mature simultaneously. After maturation the former become brittle and dry. Upon drying, they warp and break and thereby expose the leaf base to the light. Since the breaking is not at a predetermined point, a ragged rosette of papery scale bases is left. These remnants become smaller and smaller until after a time their obstruction to light and gases is negligible (Fig. 10 A).

As a rule the pines with persistent sheaths have more scales, and these are perforated to a far greater extent than is the case in pines with deciduous sheaths (Fig. 10 E, F, and G). As the enclosed portions of the needles mature, the encircling scales are frayed sufficiently to accommodate the increased diameter of needles; and the sheath, although remaining unbroken (Fig. 11 D'), is shortened until finally two-thirds or three-fourths of the originally covered portion of the leaves lies exposed.

3. Scale Number per Dwarf Shoot

In view of the possibility that the fascicle scales for the various species of pines would show numerical differences, as had been found by Engelmann (30) for the involucral scales at the base of the staminate cone, scales from the fascicles of each species and variety studied by the writer were counted and tabulated (Table 1). The extreme range is from seven, a minimum for *P. albicaulis,* to twenty-three, a maximum for *P. Torreyana.* The widest range in any one species is found in *P. palustris,* which, because of the uniformity in samples taken from several trees growing at College Station, Texas, was selected for testing the variation in scale number from place to place over the geographic range of a species. Samples taken from each of nine stations show that, on the whole, the numbers are related; but the samples taken from College Station, Texas, are far higher. Those samples from Foxley, Alabama, however, are lower than was anticipated. The cause of this wide variation may be due either to climatic conditions or to varietal differences within the species.

The widest range found among the fascicles of a single tree was in *P. rigida*, on which there seemed to be a difference in the scale number in fascicles taken from the various parts of a year's growth. This was observed also in a sample of *P. palustris* from Beaumont, Texas. The latter specimen had a summer shoot, and the fascicles which grew on this had a scale number which was less than that for the fascicles on the regular year's growth.

In order to test the variation in the scale number with reference to the position of the fascicles on the year's growth, vigorous twigs of *P. pinaster*, with a minimum of thirty fascicles on each year's growth, were selected; and ten fascicles from base, middle, and top, respectively, were removed and the scale number counted. No conspicuous differences were found (Table 2).

From the uniformity existing in the seven trees of *P. sylvestris* from Urbana, Illinois, the five trees of *P. taeda*, and the twenty-six trees of *P. pinaster* from the region around College Station, Texas, one would be tempted to conclude that the trees of a given species growing under similar conditions have a rather uniform scale number. Contradictory evidence, however, is afforded by *P. Laricio, P. Strobus,* and *P. montana.*

Although the numbers involved leave much to be desired, it is a striking fact that when grouped according to needle number in a fascicle, the two-needled pines usually have twelve scales (Fig. 31 A), the three-needled pines fifteen (Fig. 31 B), and the five-needled pines ten (Fig. 31 C). Sixteen of the thirty-two species counted, including all of those in which the total number of fascicles counted ran above three hundred, had nodes which fell at either ten or at fifteen scales per fascicle (Fig. 31 G). These numbers are equivalent to four and six turns of the phyllotaxic spiral, respectively, and are twice and three times the basic leaf number for *Pinus* as determined by Schneider (79). It is probable that further counts will show a clear-cut tendency to stabilize the scale number at ten, fifteen, and possibly at other multiples of five.

It should be pointed out that the pines with deciduous sheaths are uniformly low in scale number and that for those with persistent sheaths the scale number is high. The scale number per fascicle seems to increase with the length and diameter of the needles, the highest number being found in *P. Torreyana*, which has needles unusual as regards both length and diameter. The second highest numbers were found in the long-leaved pine, *P. palustris.*

It is too early to attempt final conclusions in regard to scale numbers and their significance, and yet there seems to be a definite relation between scale number and the deciduous habit, and between scale number and length of leaves, and possibly between scale number and leaf number.

TABLE 1.—NUMBER OF FASCICLE SCALES FOR THE VARIOUS SPECIES OF THE GENUS PINUS

Species	Variety	Locality*	Needle-number ber	Sheath condition†	Trees studied	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Av.	Modes
albicaulis E.		U.I. & J.P.M.	5	D	2	1	72	18																8
Armandi F.		J.P.M.	5	P	1			39	44	2	10	20	14											13
Banksiana L.		J.P.M.	2	P	1					7	10			1										10
caribaea M.		C.F.	2-3	D	1			6	31	4				6	15									15
Cembra L.		J.P.M.	5	D	1				2	21	45	9				1								10
cembroides G.	monophylla	A.T.							34	31	57	10											} 12
cembroides G.	monophylla	R.N.Y.					5	8	7	81	73	17	1										12
cembroides G.		A.M.			1																		12	12
densiflora, S&Z.		J.P.M.	3	P	1		5	9	28	18	23	6	1											11
excelsa W.		J.P.M.	5	D	1			10	30	32	37	9												12
flexlis B.		J.P.M.	5	D						8														10
koraiensis S&Z.		J.P.M.	5	D	7				23	5	19	142	55	28	2									10
Lambertiana D.	?	J.P.M.	5	D	1	-M- median near (10)																	13
Laricio P.		U.I.	2	P	1			2	47	48	3	20	6	11									} 13
Laricio P.		U.I.	2	P	1			1	1	4	15												13	11
Laricio P.		M.	2	P	1			3	21	45	7													11
mitis, M.		D.I.	2	P	1		1	35	20	2	1													10
monticola D.	mughus Willk.	D.I.	5	D	1				105	17	61	47	3										} 13
montana, M.	mughus Willk.	U.I.	2	P	1				5	4	11	4											12
montana, M.		E.P.C.	2	P	1																		12	12
murryana B.		C.S.T.	2	P	5	Early growth					2		10	5	2	12	55	140	16	7				17
palustris M.		B.T.	3	P	5	Summer shoot						4	8	7	16	35	14							17
palustris M.		F.A.	3	P	1						2	10		2	16		11	2					15	13
palustris M.		C.F.	3	P	1									1	3		5	2						17
palustris M.		S.A.F.	3	P	1								8	15	10	16	11							17
palustris M.		L.C.A.	3	P	1								6	26	5	20	5							15
palustris M.		G.P.M.	3	P	1							1	15	28	13	1	1							15
palustris M.		K.S.	3	P	1							5		13	25	2								16
parviflora S&Z.		J.P.M.	5	D	1		1	15	15	2		1				15	1							10
penke G.		J.P.M.	5	D	1			15	12	9	6													10

TABLE 1.—NUMBER OF FASCICLE SCALES FOR THE VARIOUS SPECIES OF THE GENUS PINUS (Concluded)

Species	Variety	Locality*	Needle number	Sheath condition†	Trees studied	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Av.	Mode
Pinaster A.		C.S.T.	2	P	26							25	198	234	191	34								15
ponderosa D.	Jeffreyi	J.P.M.	3	P	1								4	11	8	7								15
ponderosa D.	pendula	J.P.M.	3	P	1										7	18	4							17
ponderosa D.	scopalorium	J.P.M.	3	P	1								1	4	13	5								16
ponderosa D.	?	J.P.M.	3	P	1									10	17	3								15
ponderosa D.	?	U.I.	3	P	1								2	22	3							15		14
ponderosa D.	?	E.P.C.	2	P	1							16	22	11										11
pungens L.		J.P.M.	3	P	1			8	3	9	1													15
resinosa S.		S.N.Y.	2	P	1					6	37	13	12	28	27	21	8	1						12
rigida M.		J.P.M.	3	P	1				15	5	13	13												12
sinensis L.		U.I.	2-3	D	7		5	3	3	36	43	3												9
Strobus L.		U.I.	5	D	5		13	11	309	10														10
Strobus L.		U.I.	5					168																15
sylvestris L.		N.T.&	2	P	7						17		13	96	76	4							12	11
taeda L.		J.P.M.	3	P	5				4	4	3	6	3											12
Thunbergii P.		D.I.	2	P	1					25										4				22
tonyosho P.		Cal.	5	P	1			2													10	2		10
virginiana M.		J.P.M.	2	P	1	1			19	10	2					4	98	145	17	11	10	2		
Total.						1	97	339	780	466	492	393	381	558	434	194	98	145	17					

*Meaning of locality abbreviations:

A.M. ....Arizona Mountains
A.T. ....Alpine, Texas
B.T. ....Beaumont, Texas
Cal. ....California
C.F. ....Chattahoochee, Fla.
C.S.T. ....College Station, Texas
D.I. ....Dundee, Illinois
D.I.N.Y. ....Dana Island, N. Y.
E.P.C. ....Estes Park, Col.
F.A. ....Foxley, Ala.

G.P.M. ....Gulf Port, Miss.
J.P.M. ....Jamaica Plains, Mass.
K.S. ....Kingston, S. C.
L.C.A. ....Lake Charles, L.
M.M. ....Missouri Mountains
N.T. ....Navasota, Texas
P.F. ....Pensacola, Fla.
S.A.F. ....St. Augustine, Fla.
S.N.Y. ....Syracuse, N. Y.

†D = Deciduous sheath. P = Persistent sheath.

TABLE 2.—VARIATION OF SHEATH SCALE NUMBER WITHIN THE SPECIES *P. pinaster*

Tree No.	Part of year's growth counted	Scale number per sheath				
		13	14	15	16	17
1	Bottom	1	5	4	...	...
	Middle	2	6	2	...	...
	Top	...	9	1	...	...
2	Bottom	...	3	7	...	...
	Middle	2	7	1	...	...
	Top	4	6	...	...	...
3	Bottom	...	5	3	2	...
	Middle	...	7	3	...	...
	Top	...	3	7	...	...
4	Bottom	...	...	3	7	...
	Middle	...	...	...	10	...
	Top	...	...	1	9	...
5	Bottom	...	...	8	2	...
	Middle	...	...	1	9	...
	Top	...	...	1	2	7
6	Bottom	...	3	4	3	...
	Middle	...	...	2	4	4
	Top	...	...	2	6	2
7	Bottom	...	4	4	2	...
	Middle	...	...	3	3	4
	Top	...	...	1	9	...
8	Bottom	1	5	4	...	...
	Middle	3	5	2	...	...
	Top	...	8	2	...	...
9	Bottom	...	1	4	5	...
	Middle	...	...	1	9	...
	Top	...	...	2	8	...
10	Bottom	...	4	6	...	...
	Middle	...	4	5	1	...
	Top	...	3	7	...	...
11	Bottom	...	5	3	2	...
	Middle	...	5	5	...	...
	Top	...	4	6	...	...
12	Bottom	...	3	5	2	...
	Middle	...	7	3	...	...
	Top	...	3	7	...	...
13	Bottom	1	5	4	...	...
	Middle	1	8	1	...	...
	Top	...	9	1	...	...
14	Bottom	...	4	6	...	...
	Middle	2	8	...	...	...
	Top	5	5	...	...	...
15	Bottom	...	...	8	2	...
	Middle	...	...	4	6	...
	Top	...	...	3	3	4
16	Bottom	...	...	1	4	5
	Middle	...	3	5	2	...
	Top	...	...	2	5	3
17	Bottom	...	...	5	5	...
	Middle	...	...	...	10	...
	Top	...	...	1	9	...
18	Bottom	...	4	3	3	...
	Middle	...	...	3	4	3
	Top	...	...	1	8	1
19	Bottom	...	1	4	5	...
	Middle	...	...	2	8	...
	Top	...	...	4	6	...
20	Bottom	...	5	5	...	...
	Middle	2	5	3	...	...
	Top	...	5	5	...	...
	Totals	24	177	191	175	33

It may be more than a coincidence that the species with the most regular scale number (*P. sylvestris,* Table 1) is also the species which shows the most regular leaf arrangement (Table 4).

4. Axillary Structures

Tubeuf, in his classification of the buds of pines, mentions "buds in the axils of the sheath scales" but gives no detailed account of having found any in this position. In the dwarf shoots of *Cedrus* and *Larix,* axillary branching is not uncommon (Fig. 24 E, F, and G).

During the course of the present work, branched dwarf shoots were occasionally found in *Pinus,* but these seemed in every case to be due to fasciation rather than to branches having arisen from the axils of any of the scales on the dwarf shoot. The units on the dwarf shoots may, therefore, be looked upon as essentially sterile.

B. FUNCTIONAL LEAVES, OR NEEDLES

Immediately upon the completion of the sheath scale series on the dwarf shoot, there are deposited as many leaf primordia as are normal for the species. These primordia, after crowding each other and the tiny growing point of the dwarf shoot into the dome-shaped space beneath the hooded scales, become inactive and remain so until spring (Fig. 2 D and Fig. 25 F).

1. Time of Deposit

At the beginning of the present work some doubt was entertained as to whether these irregular structures were the leaf primordia or simply young scale primordia which in the spring would be followed by the deposit of true leaves. Their distinctive shapes and arrangement suggested that they were different from the scales, but it was thought that perhaps this was a consequence of their terminal position and the space relations under the hood of sheath scales. It is true that certain investigators, notably Goebel (38) and Küster (49), called them leaves; but little or no proof was offered to support these statements.

In order to get evidence on this point, counts of sheath scales were made on both the old and the new fascicles from the same shoots. In *P. Laricio, P. taeda,* and *P. Strobus,* which are representative of the two-, three-, and five-needled pines, respectively, the primordia on a young winter dwarf shoot exceed the number of scales on the mature dwarf shoot. The excess is approximately equal to the number of leaves characteristic of the species, plus one (Table 3). This indicates that not only are all scales and all needles present during the winter rest but that the growing point of the dwarf shoot is also present as a separate elevated
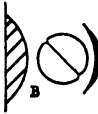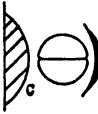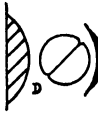
primordium. Both microtome sections (Fig. 25 F) and direct daily observations, made at the time of resumption of spring activity, have confirmed these conclusions.

The cells which are present in the resting primordium evidently enter the second phase of growth along with the tissues of the sheath scale, but there is considerable delay in extending beyond the sheath. This is due to the fact that the sheath growth is synchronized with leaf growth,

TABLE 3.—COUNTS OF SHEATH SCALES ON OLD AND NEW FASCICLES

Species	Average number of scales on 100 old fascicles	Average number of primordia on 100 new fascicles	Difference	Number of leaves plus one (growing point)
P. Laricio	10.52	13.61	3.09	3.00
P. taeda	15.27	19.38	4.11	4.00
P. Strobus	11.28	17.52	6.24	6.00
P. cembroides var. monophylla	10.75	14.00	3.25	2.00

TABLE 4.—LEAF ORIENTATION WITH REFERENCE TO AXIS OF DWARF SHOOT

Species	Tree	A	B	C	D
P. Banksiana	1	2	23	0	7
	2	0	6	28	15
P. densiflora	1	31	45	2	7
	2	20	7	0	8
P. Laricio	1	7	16	7	49
	2	5	30	20	35
	3	11	15	32	44
P. montana var. Mughus	1	35	5	45	22
P. Murrayana Eng.	1	6	5	1	20
P. Pinaster	1	60	18	20	6
	2	18	14	5	35
	3	32	9	17	9
P. pungens	1	11	13	8	21
P. resinosa	1	0	8	30	22
P. sinensis	1	50	7	0	8
P. sylvestris	1	99	1	0	0
	2	2	2	112	2
	3	60	9	0	0
	4	100	4	0	4
	5	43	37	0	16
P. Thunbergii	1	6	17	19	8
P. virginiana	1	0	25	7	1
Total		598	316	353	339

and for a time the sheath expands to accommodate the growing leaves within.

Soon the outer portions of the needles are mature and are pushed up through the scales while the tissues of the latter are still immature. From this time on, the leaves grow from zonal meristems. The leaves grow at a far faster rate than do the sheath scales, and, since the leaves fit tightly into the sheath, this growth, as long as it continues, keeps the sheath tightly extended and the scales drawn to their full extent. As soon as the leaves are mature, the shedding and wrinkling phenomena which were described above begin.

2. Leaf Orientation

In order to determine whether or not the orientation of needles is uniform for a species, certain researches were undertaken, but because of the difficulty of determining with acucracy the arrangement of the needles on the three-needled and the five-needled species, observations were confined to the pines which have only two needles per fascicle.

A sharp razor was drawn across the base of each fascicle, severing the leaves near their points of attachment. The plane of section was perpendicular to the axis of the dwarf shoot. Since the contiguous faces of the needles form a plane surface, it was found convenient to refer this *plane of needle separation* to the axial plane which passes through the long axes of both the long shoot and the dwarf shoot (Fig. 1 N).

When a twig, with its dwarf shoots cut as described above, is viewed from the apex, the lines separating the severed needles are seen to lie at various angles with reference to the axial plane (Fig. 7 G). The orientation is not constant but is rather uniform. This is especially true of *P. sylvestris,* in which five vigorous twigs from as many different trees gave a predominance of needles with their separation planes at right angles to the axial plane (Table 4). In certain cases the predominant orientation was exactly at right angles to that found on the other trees of the same species. On those twigs which showed a wide variation in arrangement, the leaves at a given level on the stem were usually oriented in the same way.

From the limited data obtained, no important general conclusions are safe. Perhaps it is not too much to suggest that some two-needled pines tend to favor an arrangement of needles in such a way that the separating plane is either parallel with the axial plane or at right angles to it. In other species the arrangement seems to be at random.

3. Leaf Fusions

Many cases of needle fusions have been reported. In fact fusions are so common that varieties with all the needles of a fascicle fused have

been established for *P. excelsa, P. Strobus, P. sylvestris,* and others (Masters, 57). Individuals with a part of their needles fused can be found in almost every species in any season. Strasburger in his famous work of 1872, *Die Coniferen und die Gnetaceen,* (87) shows figures of fused needles of *P. pumilio.* Many other cases have since been described,
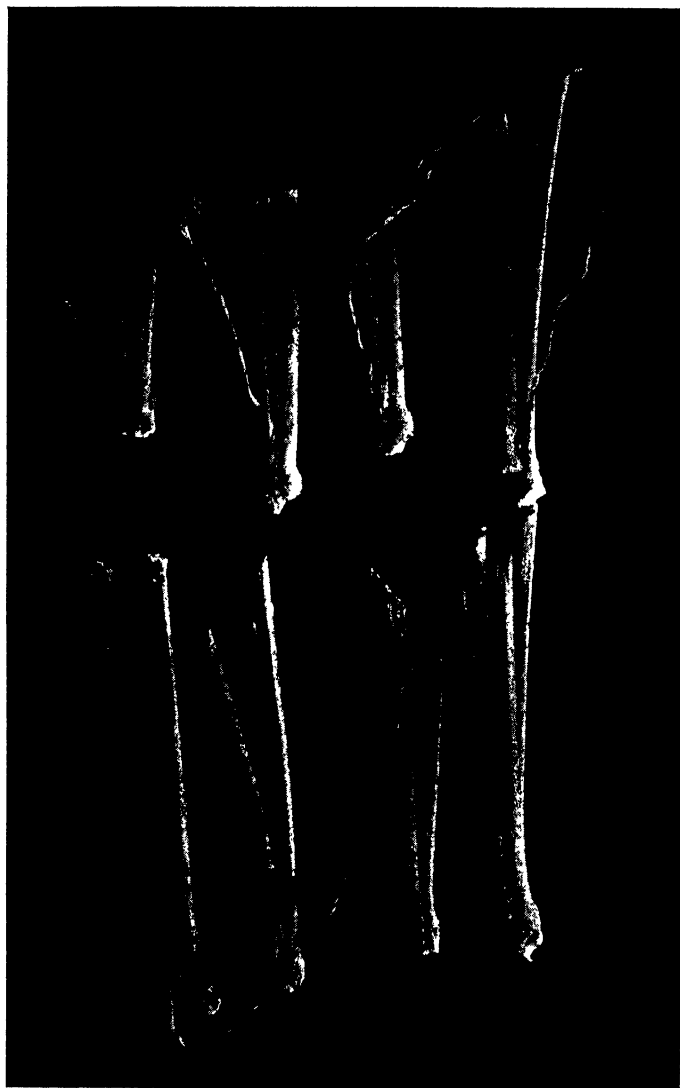

FIG. 26.—Fascicles of a normally five-needled pine with one of the needles reduced to a filamentous vestige.

and Schneider (79) has given an extensive treatment of the entire sub-
ject. Even the leaves of *P. cembroides* var. *monophylla* offer no excep-
tion to the rule of occasional fused needles. This was shown by Masters
(57) who, after describing the normal univalent needle of this variety,
described also the fused condition. He says: "There are always two
foliar tubercles only one of which is developed. In other cases . . . .
both leaves are formed but remain coherent by their edges so as to ap-
pear simple." Sir Joseph Hooker (45) found this condition occurring so
consistently in monophyllous leaves which he sectioned that he, without
discovering the simple condition, pronounced origin by fusion (welding)
as the method by which the single leaves of this variety are produced.
The three needles of *P. Nelsoni* are normally attached by their inner
angles (Fig. 27 v). A sample of *P. clausa* from Pensacola, Florida,
showed the same feature (Fig. 27 u). Perhaps all of these fusion phe-
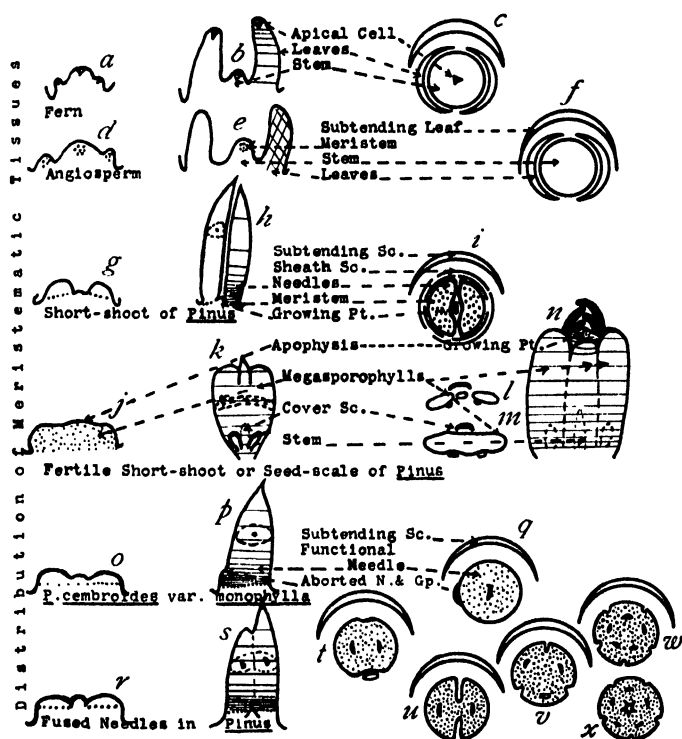nomena can be explained exactly as the welding of cotyledons was ex-

FIG. 27.—Diagram showing the author's conception of the relation between the
evolution of zonal meristems and the reduction and fusion of parts on the dwarf
shoots and cone scales.

plained earlier in this paper. Fusions, in general, seem to be the result of *meristematic recession* and *subsequent zonal growth*.

When the leaves of a two-needled pine "fuse," the growing point for the dwarf shoot may be crowded aside and remain unincorporated (Fig. 27 t); but in the five-needled pines in which all the needles are fused into a solid column, there can be but one place for the remnant of the growing point of the dwarf shoot, and that is at the distal end of the column. If the growing point had not been involved in the common upward growth, it would have remained at the end of the dwarf shoot; in this event the column would have been hollow instead of solid (Fig. 27 x).

Needles fused in nearly every conceivable manner have been described, and proliferated dwarf shoots are also common; yet no case has been reported in which the proliferated growing point for the dwarf shoot has been carried up on the fused leaves. According to Masters (57), such a case was observed for *Sciadopitys* by Carrière in 1857.

Schneider (79) contends that the fusion of the needles of pines is so superficial that it is a mistake to compare this condition to the congenital fusion of *Sciadopitys* leaves. He believes that the growing point of pines is never carried up on the leaves, and yet he shows that fusion in pines can go so far that the double point is entirely eliminated and the double vascular strand is enclosed in a single endodermal sheath. Both these conditions go beyond that normally found in *Sciadopitys*.

Since the seed scale is considered here as a dwarf shoot, we are not without our example of a transported and proliferated dwarf shoot in this genus; for Stenzel (86), Willkomm, and others have shown that the
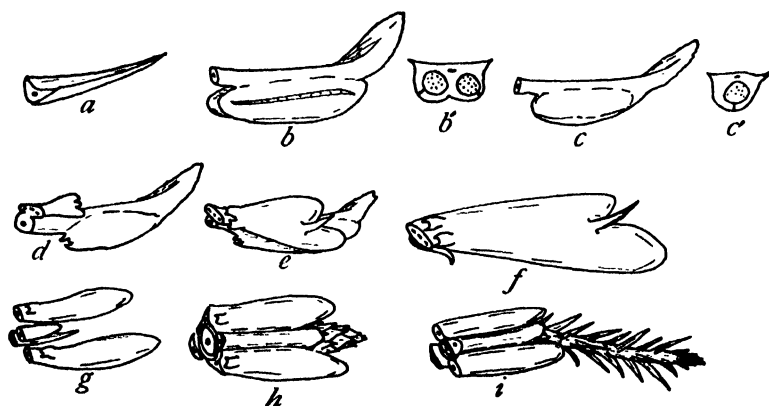

Fig. 28.—Diagram of a series of intergrading involucral bracts, microsporophylls, megasporophylls, seed scales, buds and branches found on various bisporangiate and proliferated cones of the *Abietineae*.

a, b, c, d, e, f, and g. From *Larix europea* and *P. tonyosho* examined by the author. h and i. From proliferated cones of several genera described in the literature.

growing point of the seed scale is sometimes carried up on the tip where it may make a well-developed dormant bud (Fig. 29 z and z') or even a leafy shoot (Parlatore, 68) (Fig. 28 H and I).

The sum of this evidence permits us to link leaf welding with meristematic recession and with zonal growth, and to see that the welding process can involve vegetative leaves as well as cotyledons, growing points, and other structures.

4. The One-Leafed Pine (Monophylla)

Since its discovery by J. C. Freemont, *Pinus monophylla*, now known as *P. cembroides* var. *monophylla* Voss., has been the subject of various morphological interpretations. In 1874 Bertrand (7) interpreted the leaf of this pine as a kind of twig, the vascular cylinder of which had opened and flattened out. In this he seems to have followed Meehan, who had previously (1872) advanced a twig theory for the interpretation of the leaves of pines in general as simply the subdivided extension of the dwarf shoot.

As pointed out by Engelmann (31) it was long considered probable that the terete leaf of *monophylla* was in reality a connate pair (Carrière, 18). Indeed, such double needles do frequently occur in this as well as in other pines. This fact led Sir Joseph Hooker (45) to a misinterpretation of the true relationship in *P. monophylla*. He says:

> The anomoly of the single leaf is due to the cohesion of the two semiterete leaves of each sheath and is far from a constant character. In plants at Kew the two leaves are as often free as united and on making a transverse section it will be seen that the vascular bundle in the center of the cylinder is in fact double, and that the two parts are sometimes separated.

This misinterpretation was probably caused by the tendency toward proliferations and fusions which pines undergo when subjected to exceptionally favorable conditions. *P. monophylla* at Kew is under conditions vastly different from those of its Rocky Mountain habitat.

In 1882 Strasburger (87, p. 389) called attention to the facts that the vascular cylinder of the monophyllous dwarf shoot is open and that the needle is traversed by a simple rather than a double vascular bundle. From these facts he correctly concluded that the needle is univalent. This view had also been expressed by Thomas (90).

In 1913 Schneider (79) advanced convincing anatomical evidence of a vestigal vascular strand which is present on the rim of the opening described by Strasburger. The vestige is opposite the functional vascular bundle and in the position of the vascular strand of the second needle of two-needled dwarf shoots. Schneider correctly interpreted this as evidence of needle atrophy at this point, but since he worked with mature dwarf shoots, he was unable to find any external evidence of such atro-

phied needles. Much earlier Masters (56) had seen evidences of such an abortion. He says:

> I investigated the development of the constituent parts of the leaf-bud at various stages of growth, and without going into details which are for this purpose unnecessary, I may say that the development supplied the clue which neither outward morphology nor internal anatomy sufficed to give. In point of fact, in the earliest stages examined there were always two foliar tubercles, one of which speedily overpassed the other, so that ultimately all traces of the second leaf were obliterated. . . . .
>
> The monophyllous sheath of this pine therefore owes its peculiarity to the generally arrested development of one of its two original leaves.

This observation, if substantiated with figures and detailed descriptions, would have furnished the complete story and would have prevented many later mistakes in the interpretation of the leaves of this pine. The view that the leaf of *P. monophylla* represents an aborted branch was at first adopted but later rejected by Meehan (60), who, because of further research stimulated by Newberry (65), changed over to the interpretation which holds the structure to be a single true leaf.

5. *Leaf Reduction in P. monophylla*

The presence in *monophylla* of more needle primordia on the winter dwarf shoots than ultimately come to maturity (Table 3), at once centered attention upon this variety as possibly holding the key to the manner by which the reduction in needle number in pines generally has been accomplished. Daily observations were made, and a close series of material was imbedded during the developmental stages.

As growth processes began, the growing point of the dwarf shoot and one leaf primordium (Fig. 25 D) remained inactive while the basal portion of the remaining needle began the usual meristematic activity (Fig. 25 A), pressing the differentiating point up into the crest of the hooded scales (Fig. 25 B). Soon the meristematic zone seemed to recede and to spread entirely across the top of the dwarf shoot, thus involving the inactive primordia in the general upward movement. As these were lifted into the cylindrical space within the sheath cavity, they became flattened and incorporated in the general mass of undifferentiated cells composing the functional needle. Within a short time both inactive primordia disappeared completely.

The manner by which this reduction is accomplished is strikingly similar to that by which the number of primordia is reduced during the formation of the cotyledons as previously described. Bearing in mind the suddenness with which the evidences of the manner of reduction disappear, one is not surprised that workers who examined only the mature leaves and fascicles failed to discover them.

On the mature dwarf shoots of other pines, Schneider (79) found all gradations from complete failure of a part of the needles in a fascicle to those in which the aborting needles approached the normal size and development. This frequent occurrence on nearly all pines has been amply confirmed by my own findings (Fig. 26 and Fig. 1 o). By sectioning the dwarf shoots on which these vestiges occurred, Schneider showed that in each case the atrophied trace of the vascular strand was clearly recognizable. Since he had found a similar trace on the normal dwarf shoots of *monophylla* (Fig. 23 G), he was at a loss to explain the absence of an external vestige from this variety. His conclusion was that the development had likely begun but was arrested before the rudiments became recognizable externally.

6. Leaf Reduction in Other Pines

In order to determine whether the method of reduction of the needle number observed in *monophylla* also occurs in other pines, a large number of young fascicles was examined. Many were found with needle primordia in excess of the normal number for the species under observation; but these did not occur with sufficient frequency to justify the conclusion that there would have been a later change toward a lower number, for mature fascicles with needles in excess of the normal number are common in nearly all pines. Neither microtome sections nor direct observations revealed any reduction processes in other species similar to those taking place in *monophylla*. The fact that such processes were not discovered cannot be taken as final proof that they do not occur, but rather as an indication that other methods of reduction, the evidences of which are everywhere apparent, must have accounted for most of the reduction of the needle number in pines.

The evidences that reductions in needle number have actually been going on are of such nature and number as to leave little doubt as to what the general trend has been. Summarized, these evidences are as follows:

(a) The dwarf shoot, being a specialized branch, must have evolved from a more generalized branch type. This of necessity could have been nothing other than the ordinary long shoot with its indefinite number of leaves. A rudimentary bud with partly developed leaf primordia remains as a convincing evidence of this reduction.

(b) The earliest fossil pines had numerous leaves on the dwarf shoots, indicating that the trend in leaf number has been downward.

(c) Leaf vestiges and vestigal vascular strands for aborted needles are common. The two may be associated, or the latter may be present without the former, as in *monophylla*.

(d) Varieties or specimens within a species are often found with less than the usual number of leaves, indicating that reductions are still taking place.

(e) Traumic stimuli which would be expected to bring about a return to primitive conditions cause the needle number to be increased, marking the higher number as the primitive one.

(f) Dwarf shoots often grow into long shoots with a large number of needles; and when this occurs, the branch bears simple leaves and has other features which suggest this as a primitive branch type.

(g) It is significant that of the related plants with dwarf shoots *Cedrus, Larix,* and *Pseudolarix,* which have large and indefinite numbers of leaves on their dwarf shoots, have scarcely gone beyond the pine-level in any of their characters, while *Sciadopitys* and *Taxodium* with highly specialized dwarf shoots and fewer foliar organs show a complex of characters which, on the whole, are more advanced than those of *Pinus.* This suggests that dwarf shoot reduction and specialization are associated with advancement.

7. Increases in Leaf Number

It was hoped that a careful examination of the ontogeny of fascicles on which supernumerary needles were growing would, in comparison with that of ordinary fascicles, show significant developmental differences. It has long been known that the conditions at the time of deposit and extension may influence the number of needles on the dwarf shoot, for in 1899 Bothwick (9) showed *Pinus Laricio,* which is ordinarily a two-needled species, to be capable of producing dwarf shoots with three and four needles each. For this reason *P. Laricio* was chosen for determining whether or not noticeable developmental differences occur. A tree on which less than two per cent of the fascicles normally had three needles was selected for observation of the ontogeny of supernumerary needles.

The end and lateral buds distal to the annual growth which had been extended during the summer of 1930 were completely removed during the fall of 1930. One or two of the most distal dwarf shoots on each disbudded twig, proliferated long shoots during the spring of 1931. These produced fascicles of which nearly twenty per cent had three needles each (Fig. 3 y). The ontogeny of these three-needled fascicles, however, showed nothing which in any way differed from that of pines normally producing three needles.

The increase in needle number noted above seems to point to a three-needled ancestor for two-needled pines. Similar evidence is at hand to support the view that this three-needled ancestor came down from more remote ancestors which had four and five needles.

Dr. Charles F. Hottes, of the University of Illinois, called attention to an unusual specimen of a two-needled pine (*P. Laricio*) which he had observed over a period of years. This tree was found to be covered with thousands of young twigs which clothed the trunk to a height of twenty or more feet. These twigs remain from one to a few years, then die off, only to be replaced by others of a similar nature. A detailed examination of some of these twigs revealed astonishing irregularities in needle number. To illustrate this point a description of a single twig will suffice.

In the spring of 1932 the twig in question appeared as a five-needled dwarf shoot. This shoot soon proliferated a branch with numerous units, the foliar components of which were simple with axils mostly sterile. The axils of five of these simple leaves produced dwarf shoots, and in each case these had five needles each instead of the customary pair

TABLE 5.—DISTRIBUTION OF FASCICLES HAVING VARIOUS
NUMBERS OF NEEDLES FROM TWIGS OF ONE TREE

Number of needles	Number of fascicles	Percentage of total
1	0	0
2	100	23
3	281	64
4	2	0.45
5	56	13
6	0	0

characteristic of the tree from which the branch was taken. The same twig continued growth in the spring of 1933. This season it made a growth four or five inches long, which was covered throughout with simple leaves. The axils of these leaves bore dwarf shoots, each with three needles.

A representative sample of similar unusual twigs from the same tree was gathered, and the fascicles were picked at random until a hundred normal (two-needled) fascicles had been counted. In order to obtain this number, 439 fascicles were counted. Among these the needle numbers per fascicle were found to be distributed as shown in Table 5.

The most remarkable feature was the paucity of four-needled fascicles in comparison with five-needled fascicles. The latter, although more remote from the normal, occurred twenty-eight times as frequently as the former. This suggests five as the basic leaf number and confirms the view at which Schneider arrived from a consideration of the anatomical evidence.

8. Factors Determining Leaf Number

As shown by Eichler (29), the cylindrical space within the sheath determines the cross sectional form of the needle. Needles which grow alone on dwarf shoots are circular in cross section. Sections of those grown in pairs, threes, fours, and fives make up halves, thirds, quarters, and fifths of circles, respectively (Fig. 12 a to e). Since fascicles with one, four, or six needles are relatively rare, there must be some biological reason for this numerical discrimination.

Since the sheath plays such an important rôle in shaping the cross sectional form of the needle and in making possible its unique zonal growth, one naturally turns to this organ when seeking the element of survival which has been responsible for this *trend toward certain fixed numbers.*

It was hoped that the phyllotaxic arrangement of the scales on the dwarf shoot and the arrangement of needles within the sheath would throw some light upon the probable reasons for these facts. The leaves themselves are cyclic, but the phyllotaxy of the other foliar structures on the dwarf shoot, to which series the leaves undoubtedly belong, follow the 2/5 scheme. It then becomes clear that, with the progressive shortening which was necessary in order to eliminate the internodes and produce the cyclic position, the complete elimination of the internodes from two turns of the phyllotaxic spiral would bring *five* needles into a cycle. A sixth needle, if included, would fall in line with number one and a seventh in line with number two, and so on, thus setting up interference and unequal competition within the limited space afforded by the sheath (Fig. 12 F). Doubtless the phyllotaxic arrangement, coupled with the crowding of the needles within the sheath, constitutes the major factor responsible for the preponderance of five-needled species in the genus *Pinus.*

Why the reduction should have continued below the number five is a matter for speculation. The evidence indicates that the decrease below five must have been a gradual one, the loss of needles being one by one. If this be true, the immediate forerunner of *P. monophylla* had two needles and that of *P. Laricio* and other two-needled pines had three, while that of *P. palustris* had four and so on. Prior to the attainment of the five-needled condition the reduction must have been at first erratic. As the internodal shortening proceeded and the cyclic arrangement was attained, the needles at first must have tended to stabilize at two or more whorls of five needles each, those of the outer whorl alternating with those of the inner whorl (Fig. 12 g). Ample anatomic evidence to support this view is given by Schneider (79) (Fig. 23 F).

The number of needles per fascicle varies considerably with the species and with conditions. Schneider gives a table showing these variations in a number of common species.

In seeking to ascertain the reasons for the fact that four-needled and six-needled types have proved to be less stable than those with three, two, or five needles, it was observed that in perforating the covering of sheath scales, the entire fascicle of needles pushes up as a single organ of thrust. The immediate need is for an efficient perforating organ, for the leaves must escape from the sheath before their photosynthetic work can begin. Any arrangement of needles which permits displacement at this critical stage reduces the combined efficiency and disfavors the survival of the dwarf shoot whose leaves have such an arrangement. In three-needled and five-needled fascicles, the planes of separation between the needles will permit little or no lateral movement, for each needle is wedged against the two neighboring ones; and the planes of separation are discontinuous at the central angle (Fig. 12 c and e). This is not the case in fascicles with four needles, for here each separating plane extends from side to side and permits lateral movements of the component needles (Fig. 12 d). This might possibly displace one or more young needles and prevent their united action as organs of thrust in perforating the sheath.

A search was made for evidences which would throw light upon this possibility. *P. palustris,* which has a complex sheath of many scales and which in addition occasionally produces fascicles with four needles, was selected as favorable material for a test. A search was made for those fascicles from which the needles had failed to escape or from which they had escaped with difficulty. These proved to be extremely rare. Since they usually remain on the tree for only a short time, one must examine large quantities of late spring or early summer material if fascicles with crumpled and bound needles (Fig. 19 A and C) are to be found in number. In order to find nine fascicles of them, approximately 100,000 fascicles were examined. From the same trees from which these were obtained, 5,000 fascicles were selected for determining the needle number in normal fascicles. Of the 5,000, only nine had four needles each. All of the others had two and three needles. In other words, approximately one normally developed fascicle in five hundred had four needles. Among the fascicles with bound needles, however, three in nine had four needles each. This is one in three as compared with one in five hundred for the fascicles with free needles.

Although these results are suggestive, the question of whether or not the leaf arrangement, which in its turn is a function of the leaf number, is an important factor in penetration, and consequently in survival, will await the gathering of more extensive data.

9. *Vascular Supply to the Leaves*

As shown by Schneider (79) and confirmed by Aase (1), the vascular supply to the dwarf shoot arises as two bundles which soon unite to form a complete vascular ring, from which arise the small bundles to the various scales. At the top of the ring the bundles to the leaves arise (Fig. 23 B). It makes little difference whether we are considering the hard pines in which the bundles to the leaves subsequently divide or the soft pines in which one "full bundle" without dividing supplies a single leaf. In either case we may, by combining the vascular supply from a unit of the long shoot with the vascular supply in a dwarf shoot, get an arrangement such as is shown above.

C. MERISTEMATIC TIP, OR BUD OF THE DWARF SHOOT

1. *Abnormal (Proliferated) Interfoliar Buds*

Distal to the needle attachment and resting at the tip of the dwarf shoot, the more or less inactive growing point for this modified branch is usually to be found. From the works of Schacht (77), Dixon (25), Masters (57), Penzig (69), and others it has long been known that under certain circumstances these growing points may continue activity and grow into long shoots (Fig. 5). Sections through the fascicles showing the normal unproliferated growing points were figured by Strasburger (87).

Dufrenoy (26) points out that the old functional leaves on a proliferated branch serve the proliferated branch in a manner analogous to that in which the cotyledons serve the young seedling. This is unquestionably a fact; for the original leaves at the base of such proliferated branches (Fig. 3 z) usually fall away at the close of the first year, while on the same tree the leaves on normal non-proliferating dwarf shoots may remain for four or five years. The increase in diameter of the dwarf shoot may disturb the vascular supply to the original leaves, or it may be that the expansion of a bud within causes the sheath to choke the leaves at their tender bases, resulting in death. The analogy to cotyledons seems to offer the best explanation for the death of the original leaves, for in proliferating branches a food gradient is evidently set up from old leaves to young primordia. This is shown by the arrest of growth in the leaves of branches proliferating before the maturity of the original leaves, in which case there is a direct relation between the size of the proliferated bud and the length of the accompanying leaves (Fig. 18 b).

During the course of the disbudding experiments that were previously mentioned, it was found that in *P. Laricio* var. *Austriaca* one hundred per cent of the disbudded twigs could be made to proliferate from the tips of some of their dwarf shoots, usually the most distal ones. Indeed

so regularly does proliferation occur in this species that it is possible to prune back half or more of the annual growth of each twig each season, thereby producing a small dense tree suited to rock gardens or to other plantings of limited space. On such a tree all the branches represent proliferated dwarf shoots. Just such a tree has been maintained for years at the Horticultural Rock Garden at the University of Illinois.

The disbudded twigs of *P. Strobus* proliferated twigs from their interfoliar buds to a far less extent than those of *P. Laricio*. In *P. Strobus* not more than one twig in a hundred proliferated at all, and this, during the first summer following disbudding, took the form of a scale-covered bud. In *P. Laricio* branches were often pushed out immediately without the intervention of dormant buds. Schneider (79) found that *P. Strobus* proliferated more readily than did *P. sylvestris*. Since *P. sylvestris* is more like *P. Laricio* than it is like *P. Strobus*, this observation may be taken to be the reverse of what would be expected. Very likely the ability to proliferate will be found to depend upon the age and vigor of the tree, but the writer's observations indicate that, other circumstances being equal, pines with persistent fascicle sheaths proliferate more readily than those with deciduous sheaths.

2. Normal (Non-Proliferated) Interfoliar Buds

Voluminous and interesting is the literature on proliferated dwarf shoots, but no extensive researches have been made into the normal nature and frequence of occurrence of bud rudiments on those normal dwarf shoots which never proliferate. It is true that Bothwick (10) has written a short paper on this subject, but he leaves the impression that these "interfoliar" buds occur on all of the dwarf shoots and that they are more or less invariable in make-up. Other writers dismiss the subject with but a word. Jeffrey, in his exhaustive comparison of *Prepinus stateninsis* with modern pines (47), leaves the impression that although the buds are present on modern pines, they soon disappear. He says of them: "The growing point of the short-shoot [of *Prepinus*] persisted indefinitely and did not disappear at an early stage, as in the living representatives of the genus." Other modern botanists seem to be of the opinion that such buds do not normally occur. Torrey (92), summarizing the evolution of the brachyblast, says: "Modern pines rarely have more than five needles, and have completely lost the terminal bud." In the light of these views the question of frequency, distribution, and variation of these interfoliar buds was undertaken.

A preliminary investigation showed that on some dwarf shoots no trace of the tip meristems is to be found (Fig. 7 A). When present, these growing points grade from minute simple domes of meristematic

TABLE 6.—CONDITION OF INTERFOLIAR BUDS

Species	Locality*	Tree	Number of needles	Sh.	0	1	2	3	4	5	6	7	8	9	10
Armandi	J.P.M.	1	5	D	30	10									
Banksiana	J.P.M.	1	2	P	28	2									
Cembra	D.I.N.Y.	1	5	D	0	5	10	5							2
Cembra	D.I.	2	5	D	15	1	2								
Cembra	J.P.M.	3	5	D	31	10									
clausa	P.F.	1	2	P	5	10	5	4	1						
densiflora	J.P.M.	1	2	P	25	6									
excelsa	D.I.N.Y.	1	5	D	35	22									
flexis	J.P.M.	2	5	D	20	30	5	2							
flexilis	E.P.C.	1	5	D	5	10		2							
Koraiensis	?	1	5	D	10	30	5								
Lambertiana	J.P.M.	1	2	P	15	15	2								
Laricio	J.P.M.	1	5	D	5	1	2	4	1						
Laricio	V.I.	2	2	P	12	13	16	7	3						
Laricio	V.I.	2	…	…	105	9	11								
Laricio	V.I.	2	…	…	4	35	13	1	4	1					
mitis	M.M.	1	2	P	17	15	12	25							
monticola	E.P.C.	1	5	D	45	15									
murryana	C.S.T.	1	2	P	0	2		5	4	3	1	1		3	
Pinaster	C.S.T.	2	2	P	1	3	1	4	11	16	1	1	4		
Pinaster	J.P.M.	1	2	P	6	14	12	10	5	3	2				
ponderosa	E.P.C.	2	3	P	0	6	11	10	6	2		2			
ponderosa	J.P.M.	3	3	P	0	0	3	11	23	1	3				
ponderosa	J.P.M.	4	3	P	0	0	0	5							
ponderosa	J.P.M.	1	2	P	7	6	3	1							
resinosa	D.I.N.Y.	2	3	P	5	7	4	5	3						
rigida	J.P.M.	1	3	P	0	0	5	15	6	1					
rigida	J.P.M.	1	2-3	D	2	10	21	13			1				
sinensis	V.I.	2	5	P	50	3	2	1							
Strobus	V.I.	1	2	P	65	24	11								
sylvestris	V.I.	2	2	P	76	21			3						
sylvestris	C.S.T.	3	2	P	115	8	7	2	2						
sylvestris	J.P.M.	4	3	P	119	21	27	13							
sylvestris	J.P.M.	1	2	P	35	80		10	15		1				
taeda		1	2	P	0	0	2								
Thunbergi		1		P	49	2									
virginiana															

Before transplanting. / After transplanting, 1st season. / After transplanting, 2nd season.

*The locality abbreviations are the same as in Table 1.

tissue through buds with varying numbers of secondary (foliar) primordia to well-developed scaly buds (Figs. 7 A). The latter grade off without a separating line into types already described as proliferated. There was some indication that the buds grew from year to year without being actually extended to form branches. For this reason the observations made to determine the normal interfoliar buds were always made on fascicles which were in their second year of growth.

In order to make the necessary observations, the fascicle sheaths were removed and the needles spread apart under a dissection microscope. An estimate was made of the number of secondary scales present on the primordium. Eleven classes were made. Those on which there was a complete absence of primordia were tabulated under zero (Table 6). Those on which dome-shaped growing points were present but which were without secondary scales were placed in class one. Those with a small number of scale primordia were classified according to the estimated number of their scales into classes two to nine. All others, regardless of the degree of development, were placed in class ten (Fig. 7 A).

No species was found in which growing points were entirely absent from all of the dwarf shoots. As would be expected they are less developed on the pines which have deciduous sheaths; for in order to be able to dispense with the sheath, meristematic activity in the entire fascicle, including the intercalary zones of the needles, is cut short. This arrest undoubtedly affects the adjacent tissues of the interfoliar bud. The shedding of the sheath exposes the growing point to the sun and drying air. This exposure has an adverse effect upon the bud's further development. These facts, in part, account for the usual low state of the growing point on the white pines and for the fact that proliferations for these have been so rarely reported in the literature. They explain at the same time the low percentage of proliferation obtained from the disbudded branches of *P. Strobus*.

In order to determine whether or not the interfoliar buds continue to grow over a period of years, *P. pinaster*, because of the fact that its dwarf shoots are deciduous only after several years, was selected for study.

In the fall of 1932, large numbers of fascicles were gathered from each year's growth for the years from 1928 to 1932, inclusive, approximately equal numbers being taken from each year's growth. These collections were repeated for each of several twigs from each of several trees. In order to eliminate the human element, fascicles of each age were placed in separate paper bags; the bags were then dated with concealed numbers; and after the fascicles had been thoroughly stirred, the

bags were drawn at random. The condition of 100 primordia from each bag was determined (Table 7).

The results obtained from these counts showed little evidence of any growth except for the first and possibly the second years. Buds from fascicles which were two years old were better developed than those from three, four, and five-year fascicles. Since bud parts once formed cannot

TABLE 7.—ANNUAL GROWTH OF INTERFOLIAR BUDS OF *P. pinaster*

Year	0	1	2	3	4	5	6	7	8	9	10	Mode	Average	Age in years
1928......	...	3	10	3	48	30	6	...	...	...	1	4	4.20	5
1929......	...	2	3	16	66	13	1	...	...	...	2	4	4.11	4
1930......	...	...	9	13	58	15	1	4	...	...	...	4	3.98	3
1931......	...	...	4	12	18	28	32	5	1	1	...	6	4.91	2
1932......	...	...	10	37	41	9	3	...	...	...	...	4	3.58	1

be lost and since any differential shedding over the course of years would tend, by elimination of the most weakly developed fascicles, to raise rather than lower the average bud condition, we must account for the high average on 1931 (second year) fascicles by assuming that during that year conditions for bud formation were more favorable than in the years immediately preceding.

D. BRANCH AND LEAF FORMS IN FOSSIL AND MODERN RELATIVES OF PINUS

In selecting a series of fossils with which to illustrate the steps in the probable evolution of the dwarf shoot, the task is not an easy one, for some think that pine-like characters have at times been held in common with other plants which are not abietineous. Jeffrey (47) for example says: "The occurrence of linear leaves in fascicles is in itself no real evidence of Abietineous affinity." While admitting that in some instances it might have been possible to select better representatives from the endless number of fossil relatives, the following will, nevertheless, serve our purpose.

1. Pityites

When one reads a summary of fossil Abietineae such as is given by Seward (81, Chapter 48), he is impressed with the difficulties of separating these plants into the various fossil genera. Because of these difficulties, Seward proposes the group name Pityites for abietineous fossils which cannot with confidence be referred to a more precise position. The difficulties created by the interblending of characters is well illustrated by *Pityites Solmsi*, the long shoots of which were made up of units with

short internodal components. The foliar components fell off and left persistent bases such as are met with in modern pines. The dwarf shoots were clothed at the base with scales and bore numerous (10 to 20) long needles. It is unlikely that any of the scales completely encircled so large a number of needles. If perforation occurred at all, the encircling fibers must have been broken early, and any supporting work was due either to rigid bases or to fibrous entanglements along the adjacent scale margins. The cones of this plant resembled those of *P. Strobus* or *P. excelsa.*

Some of the dwarf shoots of *Pityites Solmsi* were branched as in Larix (Fig. 24 E, F, and G) and *Cedrus,* the latter of which it resembled, though the greater length of needles is more in accordance with that of recent species of *Pinus.*

2. Prepinus statenensis

Probably the best-known fossil relative of modern pines was described by Jeffrey (46), who includes in the summary of his paper the following important conclusions:

The name *Prepinus* is proposed for this type in the belief that it is the direct ancestor of *Pinus.*

The Abietineae are the oldest living family of the Coniferales.

Pinus is the oldest living representative of the Abietineae.

From the excellent figures and the clear descriptions furnished by Jeffrey, several significant facts in regard to the morphology of this interesting fossil are manifest.

The dwarf shoot was deciduous, as is evidenced by a single annual ring associated with resin canals which were occluded by tyloses. The sheath scales were numerous, and at least the basal ones were shed, leaving marks very similar to those left where the scales of modern pines break away from a living base. Most of the scales were not deciduous, and, although there is no evidence of perforation, the crowded and angular leaves show clearly that the sheath exerted sufficient pressure upon the leaves to shape them into the available space within the sheath cavity. The reduced and distorted growing point on the dwarf shoot gives a similar testimony regarding growth pressures. The presence of a scale-like protective cover around the growing point, marks this as a bud belonging originally to a different year's growth from that of the rest of the dwarf shoot. The elongated angular leaves suggest growth from zonal meristems, and yet the continuation of resin ducts to the very base, as in the simple leaves of modern pines, hints that zonal meristems were probably less specialized than in modern pines.

The leaf trace in *Prepinus statenensis* remained undivided, resembling in this respect species of *Pinus* belonging to the section *Strobus, Cembra,* etc.

3. Fossil Pines of Modern Types

Existing in the same forests with *Prepinus*, there were pines of modern type, as shown by Jeffrey (46), who figures a transverse section through the base of a quadrifoliar dwarf shoot of one of these. This specimen, even to such details as leaf arrangement, leaf shape, and nature of sheath scale, could pass for a pine of today. The double vascular bundle in the leaves of this specimen marks it as a hard pine.

Detached leaves from bifoliar dwarf shoots of both hard and soft pines were also found in the same beds.

Solms-Laubach (84) described leaves of a *Pinus-like* plant from the Upper Jurassic or Lower Cretaceous of Bell Island. This plant had leaves which were oval or circular in outline and had the typical infolding of the walls of the mesophyll as do modern pines and cedars. The shape of the leaf made it strikingly like the leaf of *monophylla*. Solms-Laubach described the vascular bundle as being single; this would make the plant all the more like monophylla. Seward (81), after having examined some of the material, could find no convincing proof of the singleness of the bundle. He points out the fact that a second bundle may sometimes be absent in individual leaves of species normally possessing them. In speaking of this species, Seward says: "It affords an interesting example of an Abietineous type in all probability of Upper Jurassic age, exhibiting a remarkable resemblance to certain recent species especially *Pinus monophylla*."

Under the name *Pityocladus*, Nathorst (64, p. 62) describes branches similar to those of *Pityites Solmsi* and of *Prepinus*. Their occurrence as detached fossils suggests the possibility of their being deciduous, while the presence of leaves on some but not on others suggests the possibility of indifferently deciduous leaves on the dwarf shoot. This is just as one would expect in a form which was transitional between deciduous leaves and deciduous shoots.

4. Taxites

An interesting species, which Seward (81) says was first described by Nathorst as *Taxites longifolius*, shows an association of flattened and elongated leaves with scale-covered dwarf shoots. The leaves were from one to five or more millimeters in breadth and were borne in fascicles of eight or more. Such plants have been found at numerous widely separated points. Leaves of this type may be looked upon as hesitating between the abandonment of blades and the establishment of zonal meristems.

5. Pityophyllum

Seward (81, p. 380) says:

This name [Pityophyllum] is applied to detached leaves of needle-like form like those of recent pines, or to long linear leaves broader and flatter than the needles of *Pinus*. Some of the specimens referred to this genus are very similar to the leaves of Keteleeria. In a few cases the leaves are still attached to a dwarf shoot, but usually they occur as detached specimens. The genus is met with in Rhaetic strata but is especially abundant in Jurassic floras and persists through Cretaceous and Tertiary rocks. The leaves generally described under this generic term are broader and flatter than such leaves as those of Pityites Solmsi and recent Pines, and the presence of a fine transverse wrinkling on the lamina is a characteristic feature. Pityophyllum is employed for both the narrower and broader forms, and includes specimens which in all probability belong to Coniferes of more than one family. Some are certainly Abietineous but the flatter and broader forms bear a closer resemblance to the leaves of some species of Podocarpus.

6. Modern Relatives

The morphology of the dwarf shoots of *Cedrus, Larix,* and *Pseudolarix* is comparatively simple and well understood. The situation in *Taxodium,* however, is more complex. Here the portion of the dwarf shoot which is homologous to the dwarf shoot of pines is partly imbedded and may be exposed by stripping away the bark (Fig. 20). These dwarf shoots branch repeatedly from lateral buds which occur at the base of the current growth (Fig. 21).

The resulting deciduous shoots are homologous to a proliferated dwarf shoot of pine and not to the ordinary dwarf shoots as interpreted by Bernard (6). It is as if the dwarf shoot of pines should produce a lateral bud in the axil of one or both of the lateral scales and then form the absciss layer just distal to this point, later imbedding this basal remnant with its bud in the cortex of the primary branch. The following spring the lateral bud again repeats the process. Such behavior on the part of *Taxodium* accounts for the yearly crop of deciduous branches, while the production of more than one lateral bud leads to branching of the dwarf shoot and eventually to the tufts of deciduous twigs which are so characteristic of the old branches of members of this genus.

If *Sequoia* and related plants have abandoned regular annual branch-fall in favor of a more or less continuous branch-fall as hinted at by Bernard (6), it may be that in such plants the homologue of the dwarf shoot now lies imbedded at the base of the lateral branches. It is conceivable that this has been one of the ways by which the dwarf shoot has been eliminated from some members of *Pinaceae.*

These findings are difficult of exact interpretation; but for our purpose it is sufficient to point out that the forms which were characteristic of Jurassic and Cretaceous time and which persisted through the

Tertiary had leaves and dwarf shoots, each of a type through which those of modern pines must, of necessity, have evolved.

The sum of these findings calls to our attention forms with large and indefinite numbers of scales as well as large and indefinite numbers of functional leaves on the dwarf shoots, forms with indifferently deciduous leaves, with indifferently bladed leaves, with indifferently developed zonal meristems, with fascicle sheath scales serving partly developed supporting functions, dwarf shoots with partly suppressed growing points, tufts of functional leaves which approach the whorled condition, and flattened fascicled leaves unshaped by sheath pressures. Plants with these features grew side by side with others which, at this early period, had evolved characters that we now associate with the most advanced of modern pines. In short, the fossil record when combined with the better-known story of the short shoots of modern forms presents a fragmentary but readable history of the evolution of the dwarf shoots of *Pinus*.

VI. EVOLUTION OF THE VEGETATIVE DWARF SHOOT AND ITS FOLIAR ORGANS

A. LITERATURE

In treating the gymnosperms as a whole, Coulter and Chamberlain (22, p. 406), under the heading of "Evolutionary Tendencies among Gymnosperms," call attention to the fact that, "A general tendency expresses itself throughout a great group, and has to do with the transition from ancient to modern forms, rather than with the breaking up of the group into several phylogenetic lines." Certain of the tendencies to which they have called attention need be mentioned here. Their conclusion in regard to "the most obvious tendency to reduce the cotyledons to the fixed number two" has been mentioned earlier in this paper.

In discussing the tendencies of the leaf, Coulter and Chamberlain say:

It seems clear that the most ancient gymnosperms were large-leaved forms, from which the small-leaved conifers were derived and yet small-leaved pteridophytes may have been more ancient than large-leaved ones. If this be true, the appearance of small leaves among conifers is the reappearance of an ancient feature and not its retention.

Coulter and Chamberlain make no mention of internodal shortening as a general tendency, and yet this change must have accompanied the transition from macrophylly to the microphylly. Large-bladed leaves on short crowded nodes such as we find on modern pines is inconceivable. In order to prevent light interference, bladed leaves on dwarf shoots require long petioles as in *Ginkgo*. Indeed, Fankhauser (33) found a close similarity between the anatomical structure of the petiole of *Ginkgo* and

the leaf of pines. Masters (57) thinks that pine needles represent the petiolar remnant of such a leaf. The macrophyllous leaves of *Ginkgo* necessitate a sparse distribution of the dwarf shoots along the twigs (Fig. 24 B and C). These are often more than 100 times as far apart as the dwarf shoots of pines. Whether the extreme internodal shortening in the ancestry of *Pinus* occurred during or after the acquisition of microphylly is a debatable point, but it is certain that the short internodes did not precede the loss of broad blades.

Additional quotations from Coulter and Chamberlain are advisable:

The leaves of gymnosperms may be used to illustrate a structure that exhibits no general evolutionary tendency, but responds more or less directly to the conditions of living. The most ancient gymnosperms possessed ample, fernlike leaves, and under appropriate conditions this type of leaf persisted, as in the tropical cycads of today. The conifers, however, have developed a very different type of leaf, one that was well under way among the Cordaitales, and which reaches an extreme expression in small and rigid needles or concrescent scales. . . . .

It would be interesting to know the conditions in which needles and concrescent disks were established: but in the absence of any such knowledge, the sharply contrasted geographical distribution of Cycadales and Coniferales may suggest that the conditions of change were associated with the evolution of the land areas and of the climate of temperate regions.

Because of the close relationship between the various components of a stem unit, it is preferable to treat the evolution of the foliar and the corresponding internodal component together. In the light of evidences already cited, an attempt is made to outline the steps as we interpret them.

B. STEPS IN THE EVOLUTION OF THE DWARF SHOOT AND FUNCTIONAL LEAVES

1. Before the advent of branch dimorphism the forerunners of the dwarf shoots must have been simply the leafy secondary branches (Fig. 29 a). Since these were in no way different from the long shoots, the production of simple buds as described for them applied also to the laterals, thus crowding the first year's growth of the lateral shoots into simple, scale-covered, axillary buds (Fig. 29 c). Upon extension these at first must have made ordinary long shoots.

2. Further shortening involved units other than those bearing bud scales and produced a dwarf shoot with shortened annual growths (Fig. 29 f). At this level in dwarf shoot evolution, the possibility of becoming a long shoot likely depended upon position as in *Larix* and some other modern forms. The most distal branches were favored, and they alone had the opportunity to grow into shoots of unlimited growth. The remaining shoots were miniature replicas of their more favored fellows. In such crowded positions the leaves, in order to prevent light in-

terference, must have been either linear as in *Cedrus* or else lifted on long petioles as in *Ginkgo*. A reduction or loss of blades, therefore, probably paralleled this early development of the dwarf shoot. From this point the evolution of the dwarf shoot seems to have followed more than one course. We shall concern ourselves only with that leading to *Pinus*.
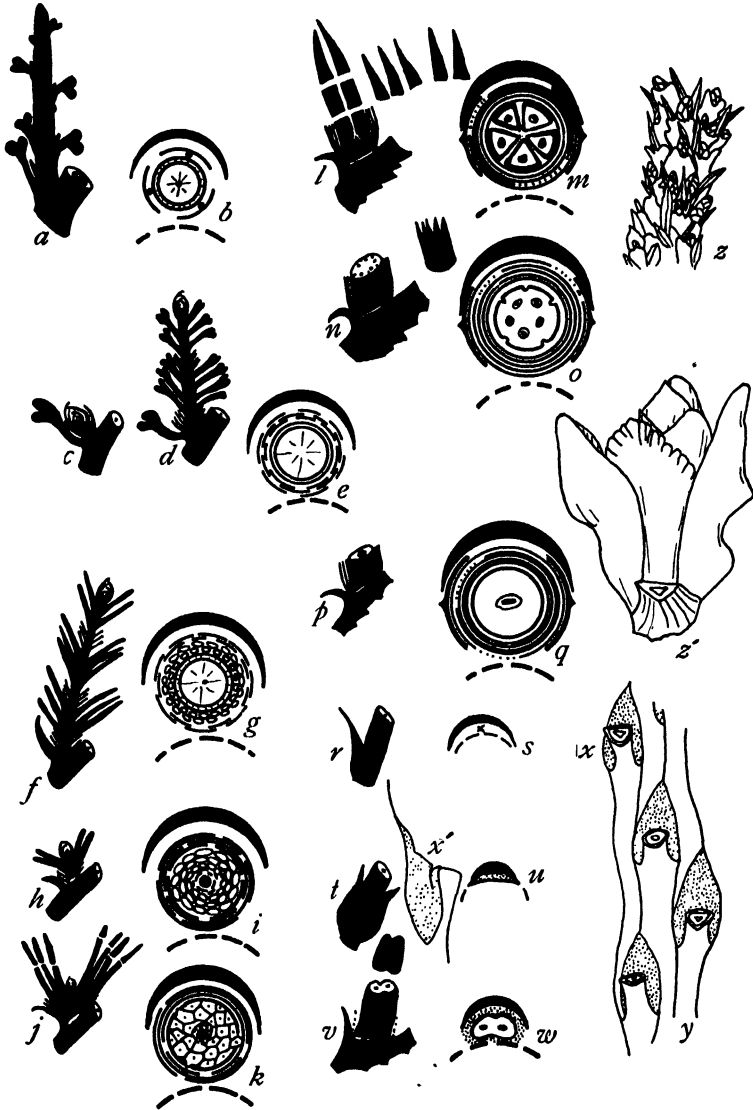

FIG. 29.—Diagrams showing the author's conception of the chief steps in the evolution of the dwarf shoot.
(See explanation on opposite page.)

3. Further shortening crowded the leaves, even after extension of their short internodes, back within the cup (forerunner of the sheath) formed by the old bud scales. This protected the leaf bases from mechanical and insect injury, and from drying, thus permitting the basal cells to remain tender and meristematic. The acquisition of zonal meristems gave the power of continued growth, thus permitting an adjustment of needle size to the season. This overcame the handicap imposed by the acquisition of compound buds, for in these the number of units for a given season is unchangeably fixed during the season prior to their functioning, so that the leaf number cannot be adjusted to later changes in climatic conditions. With the advent of basal meristems it became possible to limit or to increase the photosynthetic area without changing the leaf number.

Crowding of the leaves within the cup or sheath limited tip growth of the dwarf shoot to a single annual growth; consequently these shoots soon fell behind and were shaded off. Branch-fall came to have survival value, and the deciduous habit became fixed. With the establishment of branch-fall, it became poor economy to store much food in the dwarf

Explanation of Fig. 29

a. Hypothetical early ancestor with monomorphic branches and monomorphic leaves.

b. Section of the same showing subtending leaf in black and the position of the primary stem in a broken arc.

c. Simple axillary bud.

d. Lateral branch showing well-marked annual growth.

e. Transverse section of same showing bud scales surrounding the stem.

f. Twig similar to d, but with leaves crowded and blades lost.

g. Transverse section of same showing leaf bases within the circle of bud scales.

h. Twig similar to f, but further shortened and deciduous (white line represents absciss layer).

i. Transverse section of same showing sheath scales specialized for support.

j. Twig similar to h, but further shortened.

k. Transverse section of the same showing crowded angular leaves and reduced interfoliar bud.

l. Dwarf shoot of Pinus.

m. Same in transverse section.

n. Dwarf shoot of Pinus with fused needles.

o. Same in transverse section.

p. Dwarf shoot of Pinus cembroides var. monophylla.

q. Same in transverse section.

r. Simple sterile leaf as in Larix.

s. Transverse section of same showing sterile axil.

t. Concrescent scale leaf as in Cupressus.

u. Transverse section of same.

v. Dwarf shoot of Sciadopitys showing loss of sheath and fusion of needles.

w. Transverse section of the same.

x and x'. Exterior and sectional view of a reduced axillary seed scale on a proliferated shoot from the cone of Abies (after Willkomm). The tissues of the reduced scale render the base of the leaf concrescent.

y. Proliferated shoot from cone of Abies (after Willkomm).

z. Portion of a twig similar to y except the seed scales are well developed and each bears a bud at the tip (after Willkomm).

z'. Single unit from z but more highly magnified (after Willkomm).

shoots or to use materials in the construction of woody parts soon to be lost. Further elongation of the leaves at the expense of the shoot was the natural consequence. The tendencies toward leaf extension and shoot shortening were thus accentuated.

It is extremely unlikely that these early dwarf shoots acquired at once any of the highly specialized features such as perforated scales or whorled leaves. For this reason we would postulate for this stage in the evolution of the dwarf shoot, a short, weakly, deciduous branch whose basal bud scales supported several close spirals of leaves of the typical conifer type and whose tip formed a poorly developed scale-covered bud for the following year's growth. To put the case in other terms, this stage in the evolution of the dwarf shoot was approaching the *Prepinus* level (Fig. 29 j and k).

4. We have only to assume the continued shortening of internodes in order to arrive at the condition found in *Prepinus statenensis*. Here the deciduous habit was well established and the interfoliar bud reduced and crowded out of shape. The sheath scales were highly specialized and evidently exerted sufficient pressure upon the enclosed leaves to shape these to the cylindrical space within the sheath.

5. The compound winter bud on the long shoot had several far-reaching effects upon the dwarf shoots which in their early stages came to be enclosed within it. This enclosure relieved the scales of the dwarf shoot of the work of meristematic protection, this function having now been taken over by the primary (subtending) leaves. The scales on the dwarf shoot were thus left free to exercise their newly acquired function of leaf support. Hooding, fraying, perforation, zonal growth, and the various means for shedding the sheath now came as adaptations to the supporting function. The young buds for the dwarf shoots were crowded together within the compound bud, where competition for space was keen. Growth pressures were exerted upon the meristematic secondary shoots; their proximal scales (lateral and central scales) were displaced and flattened, and certain leaf arrangements were favored.

6. The delay which was responsible for the compound winter bud necessitated the almost simultaneous extension of the main twig, of all the dwarf shoots, and of the leaves. This in turn necessitated the formation of all these structures out of stored foods. The limited amount of growth possible from this source tended to shorten still further the internodes on the primary axis, to bring the dwarf shoots into interference with each other, and to put an additional premium upon a long-continued growth of the needles.

7. Further specialization of the sheath scales, especially the advent of perforation, increased the binding efficiency of these organs. The

leaves were crowded and their corresponding internodes shortened to extinction, and the needles were brought into the cyclic position. The cyclic arrangement necessitated a limitation of leaf number to harmonize with the phyllotaxy, and dwarf shoots with five needles or with some small multiple of five needles were favored. The acquisition of these features together with a continuation of the reduction of the interfoliar bud marked the advent of the true pines (Fig. 29 l and m).

On occasional dwarf shoots in nearly all pines and in the so-called monophyllous varieties in several species, meristematic recession involves all the leaves in a common upward growth, producing a single structure from the welding or cohesion of several leaves (Fig. 29 n and o). This carries the evolution one step beyond that attained by the group as a whole. With reference to its tip meristem and functional leaves, at least one related form, *Sciadopitys,* became stabilized at this level. In this genus an additional reducing step has been taken, for *Sciadopitys* has eliminated the scales of the fascicle sheath.

8. In some respects one variety (*monophylla*) of *P. cembroides* carries the reductions beyond the point attained in *Sciadopitys*. Here the recession involves the incorporation of extra leaves into a single functional one with but a vascular vestige of the other contributing member. Thus is produced the most highly specialized condition found in the vegetative dwarf shoots of any modern pine (Fig. 25 A; Fig. 29 p and q). The sheath, although still present in monophylla, is here reduced in number of parts and in complexity of scales.

9. There is some evidence in support of the view that shoot reduction has at some time in the past gone far beyond the point now found in either *Sciadopitys* or in *P. cembroides* var. *monophylla*. The reduction of dwarf shoots to the point of extinction is not inconceivable. If this has been the course of evolution, we should not be surprised to find fossil plants with pine-like characters but with extremely reduced phylloclads in the axils of simple leaves, or simply a proliferation of axillary tissue to produce an adhesion of leaf and stem. Following the production of such a reduced structure, the next step would be the complete loss of the axillary outgrowth. Thus by the complete elimination of dwarf shoots, pine-like ancestors may have given rise to other genera such as are now described as having monomorphic branches (Fig. 29 r, s, t, and u).

C. EVOLUTION OF THE LEAF MERISTEMS

The important steps in the phylogeny of leaf meristems which we find in pines appear to have been as follows:

1. Apical as in ferns (Fig. 27 a, b, and c). Buchholz (15) has shown that this condition is still retained in the early embryos of pines.

2. Grouped or general as in most simple leaves.

3. Basal as in the needle leaves of pines (Fig. 27 g and i).

4. Sub-basal as in *P. cembroides* var. *monophylla,* in fused pine needles, and in the seed scales (Fig. 27 j to x).
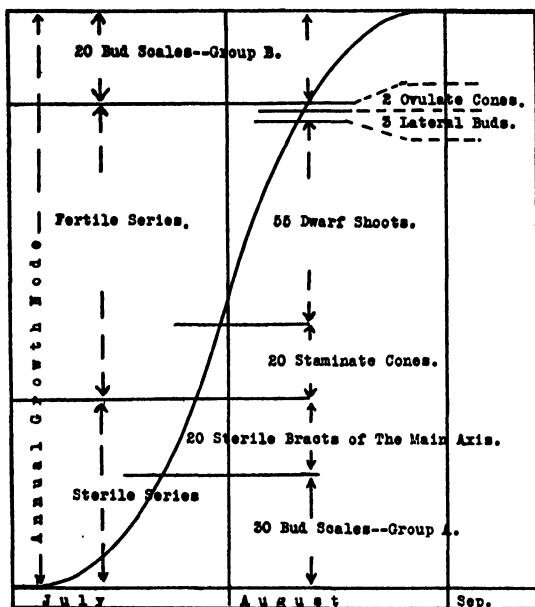

FIG. 30.—Annual curve of deposit of units on the long axis.

VII. THE OVULATE DWARF SHOOT, OR SEED SCALE

A. VOLTZIA AND THE PRIMITIVE TYPE OF SEED SCALE

Numerous fossils have been described which throw some light upon the structure of the primitive abietineous cone scale, but our discussion will be confined to the single excellently preserved specimen of *Voltzia Liebeana* which Walton (100) figured (Fig. 32, parts 4 and 5) and described in 1929.

Voltzia was obviously a conifer, the seed scale of which was woody, flattened, multisporophyllate, and transitional between the greatly reduced seed scales of modern conifers and the simple strobili (Fig. 32, parts 1 and 2) out of which the scales of both *Voltzia* and modern conifers must have evolved.

On Walton's specimen the leaf-like cover scale was unmistakably present. The constituent sporophylls of the branch-like seed scale were five in number. The first pair were opposite each other, and in both shape and position resembled the lateral scales of the vegetative dwarf shoot. Although somewhat crescent-shaped in cross section (Fig. 32 *cs*), these lateral sporophylls had their seed-bearing surfaces turned away from the cover scale and toward the axis of the compound strobilus of which they were originally a part.

The individual sporophylls each bore a single seed, which is the exact number found on the sporophylls* of members of both the *Abietineae* and Araucarineae.

The central sporophyll of *Voltzia* occupied a position exactly corresponding to that of the central scale on the vegetative dwarf shoot of *Pinus*. It was more flattened than the lateral sporophylls and was not folded, a fact which shows that the direction of pressure was along the axial plane. The apex of the central sporophyll was directed upward. The long axis, while lying in the axial plane, paralleled that of the main axis of the compound strobilus. If the central sporophyll had an opposing mate on the cover-scale-side of the axis, this was so much reduced that it remained hidden by the cover scale.

The two sporophylls that remained were flattened, sterile, and laterally placed. They occupied the concavities formed by the folding of the lateral sporophylls.

During fossilization of Walton's specimen, the growing point of the scale was hidden in such a way that the presence of a terminal-bud-vestige was left uncertain. Our experience with dwarf shoots in general and with cone scales in particular leads us to believe that a terminal bud of some kind must have been present. Reason demands the presence of such a growing point, at least during the early stages, for we cannot conceive of the presence of five well-developed foliar organs without assuming an axis out of which their early primordia were developed. We have a choice, then, of assuming the presence of an axis on the mature scale or its absence due to incorporation during the development of the scale.

With this brief description we shall leave *Voltzia* for the moment and return to it in connection with the treatment of the evolution of the cone scale of conifers in general.

B. Developmental Morphology of the Normal Seed Scale

The early developmental stages of the seed scale are amply treated by Strasburger (87, Plate V) who makes a comparative study of them as

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*The morphological sporophyll is here referred to. It is not to be confused with the seed scales.

seen in many conifers. He, from a study of the normal anatomy and development, arrives at the brachyblast interpretation of the seed scale.

In the present work the similarities between the early stages in the development of the dwarf shoot and the corresponding stages in the development of the cone scales were found to be striking (Fig. 22). The bract or cover scale for the latter, as pointed out by Strasburger (83), is without question homologous to the subtending scale of the former. Both give rise to axillary outgrowths (Fig. 22 A and F) which, because they grow from the axils of homologous organs, are themselves homologous. In both cases these axillary outgrowths in their turn give rise to a pair of simultaneously appearing lateral primordia (Fig. 22 B and G) which, by the same rule, are homologous. In other words, *the megasporophyll of the seed scale is homologous to the lateral scales of the fascicle sheath.*

The primordia for the lateral megasporophylls are more robust and appear earlier in the ontogeny of the axillary outgrowth than do the lateral scales of the fascicle sheath (Fig. 22 B and G). In *Pinus*, simultaneous meristematic activity in all three primordia of the cone scale lifts the triple-pointed structure upward until the center member finally ceases meristematic activity and matures all its tissue, thus becoming the apophysis (Fig. 22 H and I).

The lateral sporophyll primordia differentiate vascular strands and become the two flattened lateral extensions of the seed scale, and each bears a single ovule. The three fused structures collectively make up the seed scale (Fig. 28 g and f).

Since in its early stages the median member resembles the growing point of the dwarf shoot, Strasburger interpreted it as the axis of the ·dwarf shoot. The unquestioned presence of this structure demands that, regardless of whether it be interpreted as a true axis or as a third sporophyll or as some other structure, some disposition be made of it; for, while differentiating its own vascular supply, it becomes welded in as an integral part of the connate seed scale. The question yet to be settled, however, is whether the primordium and the vascular strand subsequently differentiated represent vestiges of a foliar or an axial structure. Discussion of this point will be deferred until all contributing evidences have been presented.

C. Abnormalities of Bisporangiate Cones

Ordinarily the cones of members of the *Abietineae* are monosporangiate, but numerous descriptions of exceptions ·may be found in the literature. Stenzel (86) found on one occasion in *Picea extelsa* Link:

. . . . androgynous cones, in which the male organs usually occupied the base and the female the upper part; more rarely were the male scattered amongst the

female; and still more rarely did the male form a middle zone with female above and below. Some of the bracts bore pollen-sacs.

Miss Holmes (44) describes, in one of the latest articles on this subject, a bisporangiate cone of *Tsuga canadensis* which was without transitional scales. She gives a partial summary of the literature dealing with the subject and points out the fact that similar cones have been found in most abietineous genera.

In the spring of 1932, the present writer discovered seven bisporangiate cones of *Larix europea,* most of which showed scales of various transitional and deformed types. These were carefully removed in order from the base of the cone upward, and a serial record was made of the characters of each scale.

Although bisporangiate cones in this species are not new (Bartlett, 4), it was hoped that the series of transitional scales would reveal some evidences of the morphology of the abietineous seed scale. When the scale records for the individual cones were arranged in parallel, certain very suggestive trends were apparent. Before this material could be assembled for publication, hundreds of bisporangiate cones of *Pinus tonyosho* (Fig. 14) and two cones of *P. Laricio were discovered.*

After numerous specimens of the pine material had been examined and serial records of the transitional scales on each had been made, most of the scales were observed to fall naturally into the classes which had already been made for *Larix.* The same general trends were observed here as were recorded for that genus.

The following description will be clearer if the reader will refer frequently to the series of accompanying diagrams (Fig. 28). In most cases scales of the following types were found on each cone examined and in approximately the order given:

1. At the base there were the usual involucral bracts which on normal pollen-producing cones precede the microsporophylls. In *Larix* these are green and in appearance closely approach the functional leaves (Fig. 24 G; Fig. 28 a).

2. Next in series followed the normal microsporophylls with their characteristic paired and abaxial pollen sacs (Fig. 28 b and b').

3. As the region of transition was approached, there was a strong tendency toward reduction and final disappearance of one of the pollen sacs while the remaining one tended to assume a median position (Fig. 28 c and c').

4. At about this level the pollen sacs began to produce rudimentary micropylar apparatus (Fig. 28 d) and otherwise to assume the appearance of ovules, while various aborted structures began to appear in the axils of the microsporophylls.

Above this level the behavior became far more erratic. Every conceivable type and combination of abnormal cover scale and seed scale were found. Some types appeared but once, and many others could not be fitted into any series. Most of the types, however, fitted into the regular series and were repeated on cone after cone.

Continuing our description of the regularly recurring types we have:

5. Nearly normal microsporophylls bearing micropylar apparatus on each sporangium and with rudimentary seed scales in the axils of the sporophylls, as shown in Fig. 28 (d), except with two microsporangia instead of one.

6. Cover scales with bladed portions similar to those appearing on the microsporophylls and at the same time bearing single median ovules on their abaxial surfaces and normal seed scales in their axils.

7. Leaf-like cover scales with two-lobed fleshy sterile seed scales in their axils.

8. Leaf-like cover scales with axillary structures consisting of fleshy seed scales divided to their bases (Fig. 28 g).

9. Forms similar to those described above (paragraph 8) but with the median member obviously welded into one of the members of the divided scale.

10. Forms similar to those described above (paragraph 8) but with blade-like expansions on some of the constituent megasporophylls.

11. Normal-appearing seed scales, the ovuloid structures of which were full of pollen.

12. Cover scales which in color and texture were identical with the seed scales and in some cases bore normal-appearing ovules on their abaxial surface. In one case the cover scale was so much like the two members which constituted the seed scale that had it not been for the point of the apophysis, it would have been impossible to determine which pair in the trio belonged to the seed scale. In other words, the cover scale was in the latter case transformed into a normal megasporophyll.

13. Finally the transitional zone and irregular structures gave way to normal cover scales which bore normal seed scales in their axils (Fig. 28 f). From this point to its apex, the cone was then, as a rule, normally ovulate.

The general impression gained from this array of material is that during the period of deposit of cone units, some physiological upset reversed the trend of development. Sporophylls which ordinarily would have produced two microsporangia began by stages to approach the megasporophylls in texture, in product, and in number of sporangia, and during the course of transition produced every conceivable transitional form. If, as suggested by Fujii (36), the sporophylls are at first indifferent as to type and their course is later determined by nutritional con-

ditions, the present observations are just as would be expected of a series of sporophylls formed during a period of nutritional change.

From the standpoint of the interpretation of the seed scale, it is significant that the number of sporangia per sporophyll becomes reduced to one, and that this assumes a median position at the same time that the microsporangium is acquiring micropylar apparatus and other characters ordinarily associated with ovules. The inference seems clear: the microsporophyll in *Pinus* has a pair of sporangia, while the megasporophyll has but a single sporangium. This is further attested by the presence of but a single ovule on the abaxial side of those cover scales which assume the color and texture of the seed scale. This is especially noteworthy since these cover scales were in direct series with normal microsporophylls and they in turn with leaf-like involucral bracts.

It is also significant that, at a stage during which the megasporophylls that ordinarily fuse to form the seed scale are remaining free from each other, many of them develop expanded blade-like tips, indicative of their foliar nature.

Of further significance is the fact that various constituents, which ordinarily fuse to make the seed scale, can be found as single, double, or triple rudimentary elevations, and that only two of these bear ovules.

If only one ovule is present, the point of the apophysis can usually be seen fused against the side of the unilateral scale as would be expected if one of the sporophylls had failed while the other had in the usual way become fused with the median member. If two ovules are present, they are on a scale that approaches the normal, i.e., double-pointed and flattened, or else they are on the divided halves of such a scale—indicating that the sporophylls normally fuse, but at times fail to do so.

Occasionally these divided scales have between them at their bases a third rudiment, which, with reference to the cover scale, occupies a position approaching the axillary. Since in no case this central structure bore either an ovule or a bud, the material afforded no direct evidence as to whether the central structure represented the shoot axis as proposed by Strasburger or a third and sterilized sporophyll as proposed by Celakovský. The position of this structure could not be used to argue alone for its cauline nature; for, as will be shown later, this argues equally as strongly for its sporophyll nature.

From the sum of the evidence certain facts seem indisputable. It is clear that in *Pinus* there are three parts which normally fuse to make the seed scale. Of these, the two lateral members normally bear one ovule each.* The third or median member normally makes the apophysis.

*The fact that one ovule per sporophyll seems to be normal for *Pinus* does not preclude the possibility that some members of the *Pinaceae* may have sporophylls which are multiovulate; otherwise we would have to assume an incredibly large number of sporophylls in the scales of such forms as *Sequoia* and *Cupressus*.

It is sterile, axillary in position, and therefore represents either an axis or a sterilized central sporophyll. The cover scale is foliar and is homologous to the microsporophyll; it may or may not be involved in the fusion of parts. The ovulate cone, as this evidence testifies, is a compound structure; and the seed scale is, therefore, a modified short shoot, or brachyblast.

D. Abnormalities of Monosporangiate and Proliferated Cones

It is remarkable how other teratological forms of an entirely different nature from those summarized above force us to similar conclusions with regard to the nature of the seed scale. I refer to what is commonly called proliferated cone scales. The persuasive power of these structures is well illustrated by the fact that Willkomm (102), despite his previous adherence to the placentation theory of Schleiden and of Sachs, from a study of proliferated cones of *Abies*, came to agree with the brachyblast interpretation. Botanists in general have tended to adopt this view, and in numerous instances it has been such proliferated cones which provided convincing evidence of the correctness of the theory. The literature list of such proliferated cones is a long one. It includes the following:

Parlatore—*Pinus Lemoniana* (68).
Oersted—*Picea* ? *Larix* sp., *Pinus montana* (67).
Sperk—*Cunninghamia, Cupressus lusitanica* (85).
Stenzel—*Picea excelsa, P. alba, Tsuga Brunoniana* (86).
Willkomm—*Picea excelsa* (102).
Velenovský—*Larix* (97).
Caspary—*Spruce* (19).
Celakovský—*Spruce* sp. ? (21).
Noll—*Larix* sp. ? (66).
Engelmann—*Sequoia.*
Braun—*Taxodium, Cryptomaria, Glyptostrobus* (11).

In spite of this array of evidence, not all modern botanists agree upon the brachyblast interpretation of the seed scale. Jeffrey (46), for example, apparently considers the evidence inadequate. He says (p. 337):

The view sometimes advanced that the ovuliferous scale in the Abietineae consists of a fused pair of foliar structures has apparently no evidence in its favor. It is as clearly a single leaf as is the microsporophyll.

The axillary structures which Willkomm (102) found on proliferated cones of *Abies* may be taken as representative (Fig. 19 z and z') of the scales on proliferated cones in general. This material and that found on my own bisporangiate cones of *P. tonyosho* are supplementary, for while

the former shows transitional stages between foliage leaves and cover scales, between cover scales and microsporophylls, and between microsporophylls and megasporophylls, the latter shows transitional stages between the sporophylls and true leaves and between the apophysis and the central constituent of the scale (Fig. 28 e and h).

In order to weld every link in this chain of metamorphosis from leaves through bracts, microsporophylls, and megasporophylls finally to the welded scale, it is only necessary to review the marvelous array of structures described by the workers cited above. A complete review of all the tell-tale individuals in the perfectly blending series is out of the question. We must be content with a partial description of a few representative specimens. The descriptions are taken largely from Worsdell's (104) excellent summary of this subject. He says:

In 1876 Stenzel described a cone in which in the axil of the bract a leafy bud arose, whose first two leaves were harder and browner and more erect than those of the ordinary vegetative shoot, and resembled more the seminiferous scale; they were directed somewhat towards the axis; the following pair of leaves were median, anterior and posterior [Fig. 32, pt. 20]. No ovules were to be seen. The pair of larger first leaves were often fused with the small leaves of the bud. He [Stenzel] concludes that 'the seminiferous scale of the Spruces consists of the first two leaves of an otherwise undeveloped branch arising in the axil of the bract, these leaves being fused by their posterior margins, and thus having their dorsal side directed towards the axis of the cone, and bearing each on this side an ovule.'

He [Stenzel] also possessed at this time a proliferated cone of *Picea alba*. The buds in the axils of the bracts bore, besides the two seminiferous scales fused by their posterior and gaping at their anterior margins, a posterior and an anterior scale, and one or two inner scales. In some cases the seminiferous scale was so completely fused with the anterior bud-scale as to form a single flat scale as seen from the front, but in reality its posterior margins were represented by two low ridges, visible from the inside, which did not, as in other cases, extend as far as the posterior bud-scale. As regards the characteristic projection or 'Dorn' on the seminiferous scale of *Pinus*, which Strasburger thinks is an axis, it may represent either the place of fusion of the posterior margins of the seminiferous scale, or the posterior bud-scale.

It is significant that this description of a proliferated scale could, with a few minor changes, pass for a description of the scale of *Voltzia*, for the "anterior bud-scale" here referred to is clearly equivalent, not only to the central sporophyll of *Voltzia*, but to the whole series of anterior structures shown as S' in the sketches comprising Fig. 32. The presence of "one or two inner scales" makes the resemblance to *Voltzia* almost complete.

The same kind of sports as those in *Picea* occur in *Tsuga Brunoniana*. In the latter plant, the posterior bud-scale is often as well developed as the anterior one, so that the parts of the bud all come to be united laterally into a woody structure. The axis of the bud is often more elongated into a leafy shoot.

Here again we have parts similar to those in *Voltzia* but with a pos-

terior mate for the central scale and with a well-developed terminal bud for the brachyblast.

Caspary and Oersted found cones of more than one genus which in many respects were like the bisporangiate cones of *P. tonyosho,* described earlier in this paper. Many of their cones, however, had additional developments in the form of buds on some of the central members. They thus furnished convincing evidence of the branch nature of such scales.

In the proliferated *Sciadopitys* cones described by Masters, the seed scales were replaced by the regular double needles which are generally admitted to be brachyblasts. Masters concludes: "Whatever be the nature of the so-called leaf of *Sciadopitys* [Fig. 32, part 15], it must be essentially the same as that of the seed scale of *Abietineae."*

Velenovský in 1888 described a cone of *Larix* on which one axillary bud "bore ovules on the lower surface of all its leaves" (Fig. 32, parts 1 and 2).

Certainly such proliferated scales, by the very frequence of their occurrence, argue strongly for the brachyblast interpretation of the abietineous cone. Of this, Celakovský seems to have been fully aware. In this connection, Worsdell quotes him as follows:

> In the Abietineae the seminiferous scale is "a symphyllodial structure, consisting of three fused appendages (two in Picea) of an axis, of which the two lateral are fertile carpels (reduced to sporangia) fused together to form the 'crista' of the seminiferous scale, while the third median leaf—the median knob of the first rudiment—remains sterile, and either aborts or, fused with the two other fertile carpels, forms the keel and mucro (in *Pinus*)."

This view has not been given the attention that it deserves; for, if the "anterior bud-leaf" mentioned by Velenovský is a constituent of the normal seed scale, it follows that the middle member of the three primordia on the young cone scale (Fig. 22 G) is not the primordium for the axis but rather the primordium for the central sporophyll. The growing point of the axis either has been completely suppressed or is incorporated into the central sporophyll.

There are some who, in spite of the frequent recurrence of these ativistic forms and the regularity of arrangement of their parts, still hold that such structures are meaningless abnormalities. This view is hardly tenable, for structures which occur regularly on plants of many genera and yet maintain a more or less constant form can hardly be called monstrosities, especially when early fossil forms like *Voltzia Liegeana* bring direct evidence to support the view that the observed forms represent true reversions. Careful comparison with *Voltzia* causes the doubt regarding the meaning of separated multifoliate parts of the seed scale to disappear, and the presence of buds and branches at the tips of the cone scales to become fraught with evolutionary meaning.

E. Vascular Supply and the Scale of Araucaria

In summarizing her description of the vascular supply to the cone units of *Pinus,* Aase says, "In all cases four bundles result, the lower supplying the bract [cover scale], the remaining three the scale [seed scale]." In similar terms we might summarize Aase's findings with reference to *Araucaria* by saying that, in all cases four bundles result, the lower three supplying the bract, the remaining one the scale (Fig. 23 Q to V). If the four bundles are homologous throughout, it simply means that in *Araucaria* the two lateral sporophylls instead of the central one have been sterilized, reduced, and welded into the scale. In keeping with the greatly exaggerated size of the cover scale in *Araucaria,* the lateral scales, although fused with a common structure consisting of four parts, apparently derive their vascular supply from the sides of the bundle leading to the cover scale (Fig. 23 U, V, and W).

With the idea that the functional sporophyll in *Araucaria* represents the central sporophyll, Celakovský would agree, but not to the welding in of the lateral sporophylls. Worsdell says of Celakovský's opinion in this matter: "In the Araucarieae where the seminiferous scale, bearing a single ovule, is obviously not a compound but a single organ, *the scale consists solely of the leaf* or its sporangial representative, the first leaf pair of the axillary bud being entirely absent."

Eames (28) in 1913, in a paper on *Agathis,* summarized the seed scale situation in general and concludes that, in origin, it is compound in all Coniferales; with reference to the group under special investigation he says, "Even within themselves the Araucarineae show a complete series from a form with strobilar units of a distinctly double nature to one most simple through reduction."

Sinnott (83) is of the opinion that both podocarps and araucarians have evolved from ancient abietinean stock and that the epimatium of podocarps, the ligule of araucarians, and the scale of Abietineae are all homologous structures and vestiges of axillary shoots. He thinks the simple scale of the podocarps has arisen either from the fusion of the two constituents of the abietinean scale or by the abortion of one of them. This derivation of the araucarian scale and of its one functional sporophyll component is not the same as that suggested by Celakovský; for to derive the single functional sporophyll directly from a *Voltzia-like* ancestor by sterilization of the lateral sporophylls is quite a different thing from deriving first the abietinean type of scale and then, out of this, by further reductions, deriving a simple scale with a single functional sporophyll. Sinnott's interpretation would make the functional sporophyll of *Araucaria* the homologue of one of the lateral sporophylls, while that of Celakovský would make it the homologue of the central scale.

VIII. EVOLUTION OF THE OVULATE DWARF SHOOT, OR SEED SCALE

A. LEADING INTERPRETATIONAL THEORIES

Although a brief restatement of the principal views relative to the morphological interpretation of the cone scale will probably help us to see the significance of the contributions made in the present paper, it would not be profitable for us to discuss in detail the numerous interpretations which have been placed upon this structure, for they are amply treated by Radais (71), Worsdell (105), Coulter and Chamberlain (22), and others.

The leading theories have been:

1. A calyx, Linnaeus (52).

2. An open carpel, Robert Brown (12).

3. A placental or ligular outgrowth from the cover scale, Schleiden (78), Sachs (75), and Willkomm (early works, 101).

4. Two fused leaves of an axillary branch or two leaves fused against the side of the axillary branch, Alex. Braun (11), Von Mohl (98, 99), Strasburger (87 and 88), Willkomm (late works, 102), Velenovský (97), Celakovský (20), Noll (66), Thiselton (89), Saxton (76), and a number of others.

5. The first and only leaf of an aborted axis, Van Tiegheim (96) or a simple axillary megasporophyll, Jeffrey (47).

6. A chalazal outgrowth from the ovules, Bessey (8).

In the formulation of this array of theories, nearly every known branch of botanical science has contributed arguments for or against the various views. The chaotic condition of the whole problem serves to emphasize the fact that the final solution cannot be expected to come from isolated bits of information but rather from the accumulation of evidences from many fields, and by a new evaluation of the old evidences from all fields.

By a careful examination of the list of interpretations given above, it will be seen that following the discovery of gymnospermy (1827) only a small group of workers have interpreted the cover scale as being equivalent to the sporophyll. These may be grouped together, for they would make the seed scale a simple sporophyll and the entire cone a simple strobilus. All the other interpretations would make the cover scale a subtending bract and the entire cone a compound strobilus. In all the theories in the latter group, the seed scale is interpreted as a *secondary axis of limited growth and, therefore, a dwarf shoot* (brachyblast).

The differences between the various interpretations in this group arise in the effort to decide *just how short this ovuliferous short shoot really is.*

Is it so short that the axis fails entirely and only a single sporophyll appears on the spot where the shoot disappeared, or is it just short enough for the true axis to put in its appearance and then produce in turn one, two, or more foliar organs? After all, these are but questions pertaining to the extent of shortening, and the various interpretations, excepting those of Sachs and Bessey, are seen to be not very different one from the other.

Had the various workers proposing these theories observed the comparative ontogeny of seed scale and vegetative dwarf shoot, had they seen an abundance of integrading scales and sporophylls, had they been acquainted with *Voltzia Liebeana* as described by Walton, and had they taken into account the vascular anatomy as described by Aase, Eames, and Sinnott, there is little doubt that all would have been united upon the brachyblast interpretation. None, then, would have felt constrained to
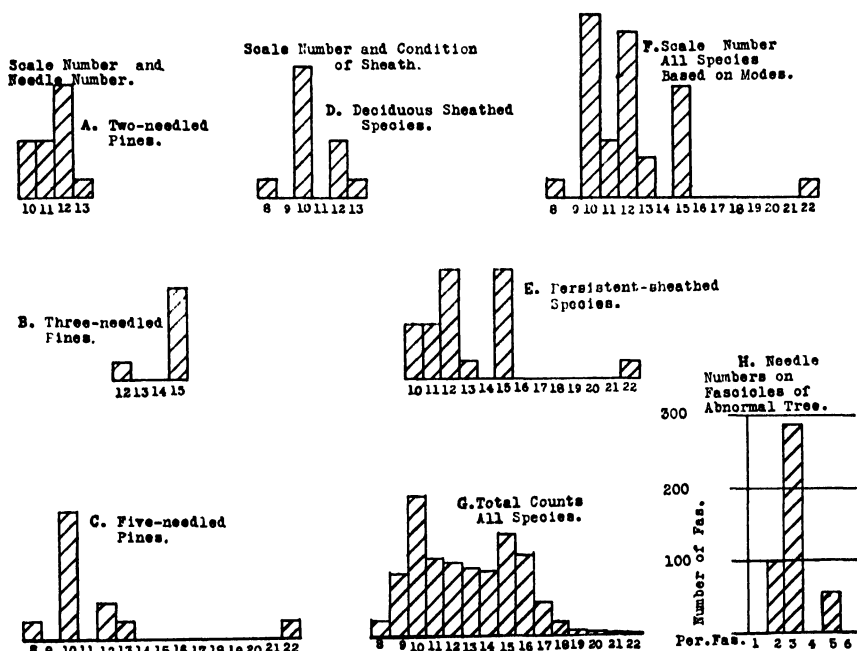
Fig. 31.—Graphs showing fascicle scale numbers in relation to needle number and persistent and deciduous sheaths.

A. Scale numbers on the fascicles of two-needled pines.
B. Same for three-needled pines.
C. Same for five-needled pines.
D. Scale number on the fascicles of pines with deciduous sheaths.

E. Same for pines with persistent sheaths.
F. Scale number on all species based on nodes.
G. Scale number on all species based on total counts.

defend a set number of sporophylls as having been retained by all conifers, but instead would have been free to admit of variations in number of constituent sporophylls in the seed scale. In *Araucaria* this number is made up of one functional sporophyll with vascular remains of two others; in *Abietineae* it is made up of two functional and a single vestigial sporophyll with frequent reversions to more; in *Voltzia* the number is three functional and two vestigial. The whole range of forms marks out tendencies which point unmistakably to lost forms with a large and indefinite number.
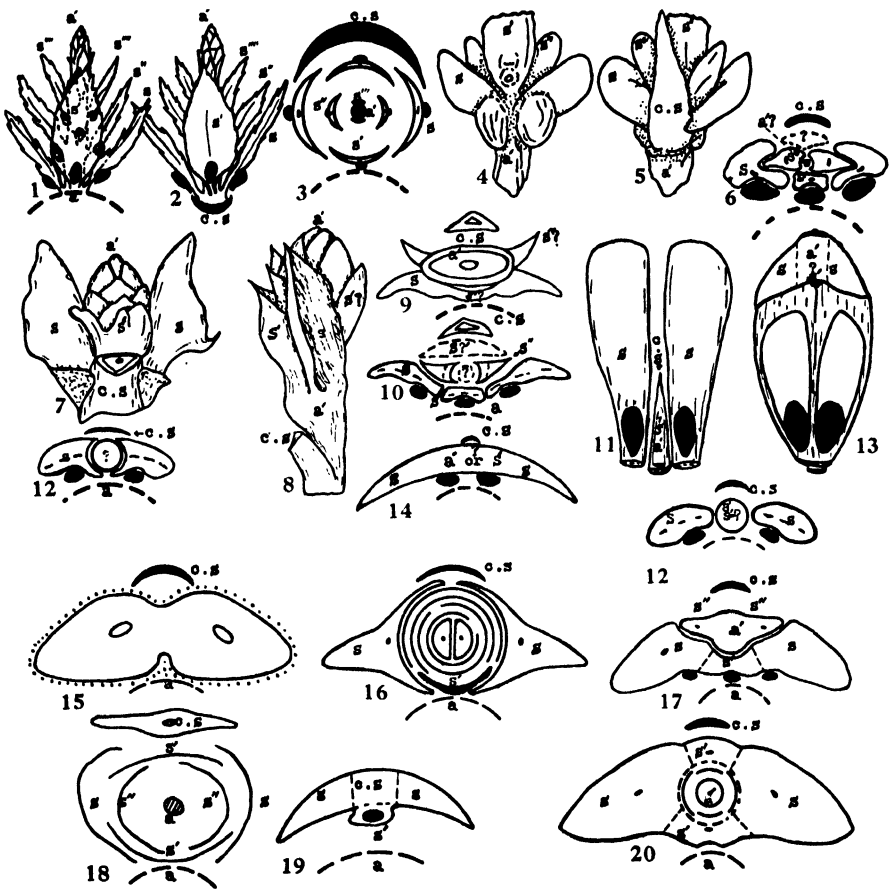
Fig. 32.—The author's conception of the chief steps in the evolution of the cone scale. The lettering throughout is uniform, *a* representing the cone axis and *a'* the axis of the simple strobilus or cone scale, *c.s.* the bract or cover scale, and *s, s', s''*, etc., the various sporophylls. (See explanation on opposite page.)

B. Summary of Steps in Cone Scale Evolution

In order to see how the seed scale may have been phylogenetically produced, one has but to assume a repetition here of processes known to have taken place in other parts of such plants as the pine.

1. The same foliar reduction processes which have for geological ages been operating on the vegetative dwarf shoot of *Pinus* and related forms have operated also upon the ovulate dwarf shoot, reducing its foliar organs (sporophylls) to a single functional pair.

2. The same internodal shortening (to disappearance), which brought cotyledons and functional leaves into cyclic positions, and the lateral scales of the vegetative dwarf shoot into positions opposite each other, has, in an analogous manner, brought the first foliar pair on the ovuliferous dwarf shoot into basal positions directly opposite each other.

3. The same pressure between subtending leaf and main axis which flattened the base of the dwarf shoot and displaced the three most proximal of its attached foliar organs, has here flattened and displaced the sporophylls.

4. The same meristematic recession which involved in a common intercalary growth the adjacent cotyledonary primordia on the embryo, the adjacent leaf primordia on fascicles of fused needles, the adjacent leaf and growing point primordia on the dwarf shoots of *monophylla,* has here again produced a compound ("fused") organ.

5. The same process of incorporation by maturation, which eliminated extra cotyledonary growing points from the embryo, and extra leaves as

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Explanation of Fig. 32

1 and 2. Front and back views of the hypothetical early simple strobilus.

3. Transverse section of the same.

4 and 5. Front and back views of *Voltzia Liebeana* G. (redrawn and relabelled from Walton).

6. Probable transverse section of same with the shed seed and the axis supplied.

7, 8, and 9. Back, side, and sectional views of typical cone scales from the proliferated *Abies* cones described by Willkomm (redrawn and relabelled from Willkomm).

10. Same but with axis reduced, fused parts separated, and with seed supplied.

11. Scale of *Pinus tonyosho* which by the failure of the usual fusions shows the separated constituents of the scale.

12. Transverse section of the same.

13. Mature seed scale of *Pinus Lambertiana.*

14. Transverse section of the same.

15. Diagram of section through base of the double leaf of *Sciadopitys* showing the absence of central and lateral scales.

16. Diagrammatic section through base of dwarf shoot of *Pinus.*

17. Diagram of Sperk's abnormal scale of *Cunninghamia* as described by Worsdell.

18. Diagram of Caspary's abnormal abietinean scale (relabelled from Worsdell).

19. Diagram of araucarian scale.

20. Diagram of a scale from Stenzel's abnormal cone of *Picea* (from his description).

well as a superfluous growing point from the dwarf shoots of *P. monophylla,* has here eliminated extra sporophylls and the growing point of the ovulate dwarf shoot.

From forms with numerous widely separated sporophylls displayed in simple strobili, the evolution of the cone scale gave rise to forms with successively shorter and shorter axes and with fewer and fewer sporophylls.

Voltzia with its fertile lateral pair of sporophylls, its fertile central sporophyll, and its sterile vestiges of more distal sporophylls, represents but a step in the shortening and reduction processes.

From *Voltzia*-like forms, evolution followed two lines. In one case, reduction and fusion of parts and the sterilization of the lateral sporophylls gave rise to a single-seeded scale containing but one functional sporophyll which, however, became an integral part of an apparently simple seed scale as in Araucaria. This superficially simple seed scale has been derived from the welding of the bract, two sterilized lateral sporophylls, and a functional central sporophyll.

In the line leading to the *Abietineae* the *retention, modification,* and *welding* of the primary pair or lateral sporophylls together with the sterilization of, and in some cases the loss of, the central sporophyll, gave rise to the scale as we now find it in this group.

C. ADVANTAGES OF THE BRACHYBLAST INTERPRETATION

This view has the following advantages:

1. It is in keeping with the views held by the most careful workers in the field.

2. It brings into harmony many of the apparently conflicting views of previous workers by showing these views correct as far as they go; for in the absence of complete information regarding the details of development, partial interpretations should be regarded as incomplete and not necessarily as incorrect.

3. By this view the two most characteristic structures found in *Pinus,* i.e., the dwarf shoot and the seed scale, become homologous and explainable by the same evolutionary tendencies.

4. It accounts for all the primordia which appear in the axil of the cover scale.

5. It homologizes the microsporophylls and megasporphylls as well as the axes upon which these are borne.

6. It is in agreement with the finding of buds, dwarf shoots, and leafy shoots in the axils of the cover scales and makes intelligible the widespread occurrence and regular form of these structures.

7. It lends meaning to the divided, partly-fused, and triple-pointed scales on bisporangiate and proliferated cones.

8. It derives the abietineous and the araucarian cone scales from a common type and points to known structures to explain the vascular anatomy of both.

9. It makes intelligible the finding of single ovules on the lower surfaces of foliar constituents of axillary buds and explains why, when the bud is suppressed, the two lower sporophylls "orientated themselves" with reference to the axis (Velenovský, 97).

10. It lends eloquence to the otherwise discordant *Larix* cone described first by Velenovský, one scale of which bore "besides the two fleshy placental lobes, five other fleshy ovule-bearing scales," and makes this scale and the short statement about it speak clearly for the branch origin of the scale.

11. It is in keeping with the finding of multisporophylled seed scales in early fossil gymnosperms and points, for the origin of both araucarian and abietinean cones, to a type the existence of which is well established.

12. It fixes well-marked tendencies which will account for the conditions found in the cones of *Sequoia, Cupressus,* and *Taxodium* without involving additional processes; for a continuation of internodal shortening coupled with meristematic recession would certainly soon involve the primordium of the subtending scale (cover scale) in the common upward movement and in the fusion. It is conceivable that incorporation by maturation might also apply to this primordium, thus accounting not only for the fusion of seed scale and cover scale but also for the disappearance of the latter from those forms in which little or no trace of it can be found.

IX. THE PHYLOGENY OF THE PINACEAE

No doubt the members of the family *Pinaceae* have had a common ancestor, and since the *Abietineae,* the oldest tribe in this family, show a strong leaning toward dwarf shoots, it is likely that the common ancestor had dwarf shoots. This is evidenced by the fact that four of the nine genera in the *Abietineae (Pinus, Cedrus, Larix,* and *Pseudolarix)* have this feature. In *Cedrus, Larix,* and *Pseudolarix* the dwarf shoots are of a rather generalized type, and on the whole the associated characters are primitive.

Three of the eight genera in the tribe *Taxodineae (Sciadopitys, Taxodium,* and *Glyptostrobus)* have dwarf shoots, and in every case these unquestionably represent extremes of dwarf shoot specialization. These are on the whole associated with more advanced characters than are the dwarf-shoot-bearing members of the *Abietineae.* The more advanced tribe of *Cupressineae* has ten or eleven genera with no vegetative dwarf shoots among them. The evidence suggests that the common

ancestor of all *Pinaceae* had spur shoots of a non-specialized type and that such branches have been lost from most of the genera and have become highly specialized in the majority of those which have retained them.

We find ourselves projecting the established evolutionary trends of *shortening, recession, elimination,* and *meristematic fusions* against the background of the *Pinaceae* and inquiring as to what characters would show in a line of plants in which the tendencies to reduce the dwarf shoot had brought this structure to the vanishing point towards which we have seen it so steadily carried. One has but to strip the dwarf shoots from a pine in order to see what type of plant would be produced by the loss of these organs. Our hypothetical plant can then be constructed by applying to this "disbranched" pine the tendencies already well established.

The leaves of such a plant would certainly be microphyllous, even scale-like (Fig. 29 r and s), as occur almost universally in the family *Pinaceae.* The axils would be for the most part sterile, and those which remained fertile would produce long shoots with probably an occasional reversion to the dwarf shoot condition as found in *Abies, Pseudotsuga,* etc. Conservative portions of our hypothetical plant, especially when wounded or otherwise unduly stimulated, would be expected to show some trace of the ancient dwarf shoot character, as do the seed scales of all *Abietineaeous* cones and the cone axes of proliferated individuals from many genera. The trend toward internodal shortening would no longer be hampered by the necessity of keeping the dwarf shoots properly distributed. This shortening, if continued, would lead to the complete elimination of internodes, thus producing opposite and cyclic leaves just as we find in the *Cupressineae.* With the axillary shoot eliminated and the primary leaf alone remaining, further fusions by intercalary growth could do nothing except to produce adnation of the primary foliar organ with the internode of the primary axis. Indeed the presence of a trace of the old dwarf shoot meristem in the axil would be expected to favor such a course (Fig. 29 x, x', and u). This would produce a concrescent leaf as in certain members of the *Cupressineae* (Fig. 29 t and u).

It is clear that, instead of describing a hypothetical plant, our description fits well the features associated with higher members of the family *Pinaceae.* So numerous and varied are the points of agreement that on a basis of dwarf shoot evidence alone, we can safely assume that evolution of the *Pinaceae* has been from a common ancestor with generalized dwarf shoots as in *Cedrus,* through forms with more and more highly specialized dwarf shoots as in *Prepinus, Pinus, Sciadopitys, Taxodium,* etc., to forms from which the dwarf shoots have been eliminated as in *Abies, Pseudotsuga,* etc., and finally to forms with opposite and concrescent leaves as in *Cupressus.*

For phylogenetic purposes it is unsafe to consider dwarf shoots, or cone scales, or any other single structure alone. One should rather consider all the known characters of the organism with which one is working. Sinnott's work on *Podocarpus* (83) well illustrates this fact. He effectively compares the characters of the *Abietineae* and *Podocarpineae* to support the derivation of the fruiting structures of the latter from the cone scale of the former and to argue for connecting these two groups on the phylogenetic tree. The mass of evidence would support such a connection, and yet we prefer to leave open the question of where to connect the line leading to the *Podocarpineae* until we know more definitely whether the single functional sporophyll of *Podocarpus* represents the central sporophyll or one of the lateral sporophylls.

In nearly all forms the evolution of the vegetative dwarf shoot and that of the ovulate short shoot have gone hand in hand. Forms like *Larix* and *Cedrus* have primitive short shoots associated with relatively primitive seed scales; *Sciadopitys* and *Taxodium* with highly specialized short shoots have advanced cone scales; and forms like *Cupressus, Juniperus,* and *Araucaria,* from which the dwarf shoots have been lost, have the most highly specialized cone scales found among the members of the *Pinaceae.*

From this general agreement between the evolution of the dwarf shoot and the seed scale, only *Picea, Tsuga, Abies,* and *Pseudotsuga* are out of line, for these forms, although devoid of short shoots, still possess seed scales which are at the *Pinus* level. Since the bulk of characters for these plants is primitive, it is necessary to assume that while advanced in one character they have remained primitive in many others.

Our conclusions with reference to phylogeny are: that the *Araucarineae* and the *Abietineae* separated early from a common ancestor; that there is some doubt as to which of these lines gave rise to the *Podocarpineae* and *Taxodineae*; that among the *Pinaceae, Cedrus* and *Larix* are low, *Prepinus* and *Pinus* intermediate, *Sciadopitys* and *Taxodium* high, and *Cupressus* the highest in position.

X. SUMMARY

1. A study is made of the axial and foliar systems of about thirty-five species of pines and of a few related plants.

2. The constituent units of the tree are described in their order of appearance.

3. The ontogeny of the cotyledons supports the view that polycotyledony is a primitive character and that fusions, incorporations, and reductions mark advances.

4. The natural and abnormal occurrence of simple leaves is treated, and their artificial production through wounding is demonstrated.

5. In the ontogeny of the bud scales it is shown that the interlocking fringed margins are the product of several factors including a hooding of the primordium, an angular arrangement of the marginal tissues, and the expansion of underlying parts which in some cases actually perforate the overlapping scales.

6. A technique is described whereby the number of bud scales and of sterile bracts can be approximately determined prior to extension of the buds which contain them. This technique is utilized in following the time of origin of units within the bud.

7. The bud scales are divided into groups "A" and "B" based upon the time of origin and upon the amount of extension of their respective internodes.

8. The expansion of the winter bud into the annual growth is described.

9. Normal and abnormal sequence of deposit is followed, and evidence is given supporting the view that the so-called lateral cone is an ecologic rather than a fixed character.

10. The staminate cone axis is considered homologous to the dwarf shoot, and the ovulate cone axis homologous to the long shoot.

11. Seed cones with proliferations and abnormal sequence of units are described, and the nature of their abnormalities is used to support the theory that they represent modified long shoots.

12. The ovulate cone is considered a compound strobilus, and the cone scale a simple strobilus.

13. The origin of concrescent leaves is associated with the disappearance of dwarf shoots from the primary axes.

14. The ontogeny of the dwarf shoot and of its foliar organs is given in detail and the following facts established in regard to them:

a. The first two scales are laterally placed, opposite each other; and the first three are distinct from the other scales.

b. The encircling sheath is produced by the perforation of the scales and the exaggerated overlapping of the scale margins.

c. The dwarf shoot spends the winter rest in full possession of all of its foliar structures including the needles.

d. Both scales and needles grow from basal (zonal) meristems.

15. In the pines which have deciduous fascicle sheaths, the shedding of the scales involves the loosening of the cohering portions and the detachment of the scales from the shoot. These steps are accomplished differently in the different pines.

16. The pines with persistent sheaths crumple these until they cover

only one-fourth to one-third as much of the leaves as when fully extended.

17. The scale numbers per fascicle from representative samples of thirty-two species and several varieties have been counted and the results tabulated. The numbers are too variable to be of much taxonomic value, but certain tendencies are manifest, notably the tendency to stabilize the scale number at either two or three times the basic leaf number (2×5 or 3×5).

18. The early ontogeny of the leaf is given, and its manner of perforating the overlying sheath is shown.

19. The orientation of the needles within the sheath is not a constant character but in some species approximates constancy.

20. The needles are found to fuse in various ways.

21. Fusions are linked with internodal shortening and meristematic recession.

22. The ontogeny of the dwarf shoot of *Pinus cembroides* var. *monophylla* is essentially like that of other pines except that only one of the two original leaf primordia comes to maturity, the other needle, together with the growing point of the dwarf shoot, being usually incorporated into the functional leaf but without differentiation of vascular tissues. Similar incorporations were not found in other pines.

23. Dwarf shoots on disbudded branches showed an increase in the number of leaves, thus marking the reduced number as a derived character.

24. The basic leaf number of needles is five. This is equivalent to two turns of the phyllotaxic spiral.

25. A theory of interference is advanced to account for the tendency toward stabilization at five needles.

26. Inefficiency in perforating the sheath scales has probably disfavored stabilizations of pines with four needles.

27. A growing point or interfoliar bud is present between the needles of most of the dwarf shoots in all the species included in the study.

28. The degree of development of these buds depends both upon the species and upon the conditions of growth. They develop least in the pines which have deciduous sheaths.

29. Disbudding of the long shoots induces proliferation of some of the interfoliar buds on the more distal dwarf shoots.

30. Numerous abnormal (bisporangiate) cones of *Pinus* and *Larix* are described in which the ovuliferous scales show non-fused and transitional conditions which, in general, support the brachyblast theory.

31. The brachyblast theory of the cone scale is strengthened by the fact that the early ontogeny of the dwarf shoot proves to be almost identical with that of the cone scale and by the fact that the three most

proximal and most regularly placed scales on the dwarf shoot all have similarly placed counterparts on the cone scale.

32. The two sporophylls on the seed scale correspond to the lateral scales on the dwarf shoot.

33. Some of the fossil relatives of *Pinus* are reviewed.

34. The dwarf shoot of *Pinus* is found to be homologous with the persistent basal (imbedded) portion of the shoots of *Taxodium*, the deciduous portion of which corresponds to proliferated pine fascicles. It is pointed out that a discontinuation of the habit of seasonal branch-fall may have given rise to forms like *Sequoia*, in which the true homologue of the dwarf shoot of *Pinus* may have disappeared simply by being imbedded and by having its habit of shedding discontinued.

35. Most of the unique vegetative characters in *Pinus* can be directly or indirectly attributed to influences incident to the formation of the compound bud. This structure relieved the sheath scales from the work of meristematic protection and permitted specialization along other lines. It necessitated the almost simultaneous development of many structures from stored food and exerted shaping pressures upon the enclosed immature dwarf shoots.

36. Tentative steps in the evolution of the leaf meristems of pines are presented as follows: (a) apical, (b) grouped, (c) basal, and (d) subbasal (in certain special cases).

37. The early common ancestor of the *Pinaceae* probably was macrophyllous and had monomorphic branches.

38. The formation of dimorphic branches accompanied the transition to microphylly, and the development of the two was probably interdependent.

40. The disappearance of the dwarf shoots and a continuation of the tendencies toward internodal shortening are postulated as explanations for the appearance of abietineous forms with opposite, whorled, and concrescent leaves.

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JOHN THEODORE BUCHHOLZ   FRED WILBUR TANNER

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A MONOGRAPHIC REARRANGEMENT OF LOPHODERMIUM

WITH FIVE PLATES

BY

LEO ROY TEHON

ACKNOWLEDGMENTS

INTRODUCTION

FUNGI of the genus Lophodermium are of interest from two primary points of view. First, since many species inhabit leaves of evergreen trees and either cause or are closely associated with premature falling of the needles, they have been the subject of much investigation as factors concerned with economic destruction. Second, because of their heterogeneity of morphological characters, species of the genus have within recent years come to have a very uncertain position in the system of mycological taxonomy.

It is not the purpose of this paper to undertake a discussion of the economic aspects of the genus. Several investigators, notably von Tubeuf (1888, '95, 1901, '08, '10)* in Europe and Darker (1932) in America, have brought together this information so far as the conifer-inhabiting species are concerned. Of those species that inhabit grasses, probably none is economically important; and this is true also of the species that inhabit other monocotyledons and the dicotyledons. It is characteristic of species on all plants other than conifers that their fructifications either are not developed until the life of their host is ended or are developed only just before or sometime after the leaves of dicotyledonous hosts have fallen. Since the number of species on coniferous hosts is smaller than the number on monocotyledons and dicotyledons, and since even among those on conifers some are recognized as saprophytic while for others there is often very little proof of pathogenicity, the genus is to be regarded as made up of a preponderance of saprophytic forms.

The taxonomic relations of Lophodermium, with which this paper is especially intended to deal, have not been well investigated. The Hysteriales, to which Lophodermium has been assigned, have been given so little attention that Gäumann, in his "Comparative Morphology of Fungi" (1928), has been able to give only a page and a half of discussion to the entire order. According to this authority the Hysteriales are Pyrenomycetes with elongated perithecia which are closed during development and which open at maturity by means of a long slit that follows an earlier developed dehiscence line. Characteristically, the hymenium is completely uncovered at maturity.

The elongate opening is a character possessed also by the Lophiostomataceae of the Sphaeriales; and it is the opinion of von Höhnel (1918) that on this account these two groups should be united in an Order to which he has given the name Hysterostomeae. In this treatment, the ma-

*Year numbers, with or without parentheses, following an author's name refer to articles listed under his name in the Supplementary Bibliography (p. 124).

jority of the Hypodermataceae are, however, removed to the Phacidiales (in von Höhnel's sense, strictly) and are there redistributed in a number of new families.

In both views, the taxonomic position of Lophodermium is determined on the basis of such simple characters as the fact that the fructifications are imbedded in the host tissue, that they are elongated, and that they open by a longitudinal slit. Neither the morphology nor the ontogeny of the genus (nor, indeed, of the order) has been sufficiently investigated to give any adequate basis for a satisfactory placement of the heterogeneous forms included in it.

As a basis for the treatment given in the following pages additional facts will be presented, bearing upon the morphology of the hysterothecium. It has, however, been impossible with the material at hand, to add to or to substantiate the meagre information already furnished by Killian and Likhité (1924) and by Likhité (1926) on the ontogeny of the genus. This is a field in which further investigation would be very well repaid.

Among the named species of Lophodermium a large proportion are represented by a very small number of collected examples—many, in fact, only by the type specimens. These are often difficult to secure, because types have not been preserved, because the place of preservation has not been recorded, or because of disorganized conditions in the herbaria in which they are kept. The following is a list of such species, which are necessarily omitted from consideration in the body of this paper.

1. Bolivarii Frag.
2. Calami Henn. & Nym.
3. Canangae Henn. & Nym.
4. cedrinum Maire
5. Clithris Starb.
6. Empetri Rostrup, in litt.
7. Epimedii (Ces.) Sacc.
8. Gentianae Vogl.
9. intermissum Starb.
10. iridicolum Petrak.
11. Luzulae Hazsl.
12. montanum Ferraris
13. Neesii Duby
14. Oxycocci (Fries) Karst.
15. proximellum Mout.
16. Sacchari Lyon
17. sphaerioides (deAlb. & Schw.) Duby
18. Spiraeae Hazsl.
19. Theobromae Pat.
20. tjibodense Henn. & Nym.
21. tumidulum Sacc.
22. velatum Berk.
23. Vrieseae Rehm

HISTORICAL REVIEW

Lophodermium was established as a genus in 1826 by F. F. Chevallier (1826) in his "Flore général des environs de Paris." In classifying the fungi of his vicinity he divided them into 14 classes. The twelfth of these he named Cheilomyci, and in this he included a single order to which he gave the name Hysterineae. There were included in the order four genera: Lophium Fries, Hysterium Tode, Lophodermium Chevallier,

and Schizoderma Chevallier, not Ehrenberg.

As a characterization of the class Cheilomyci, Chevallier gives the following:

Fungi Sclerotiaceis *epiphytis et* Phacomyceis *quodam modo intermedii plerumque epidermide arborum corticis et plantarum erumpentes, coriacei compacti demum saepe excavati friabiles, disco bilabiato insigniti, labiis plus minusve tumidulis sulcoque longitudinali simplici aut crista prominente mediantibus. Asci erecti adfixi in pluribus paraphysophori; sporulae minutae subglobosae nec didymae.*

By way of further definition, he gives the following characterization of the order Hysterineae:

Species simplices bilabiatae ut plurimum hypogenae coriaceae nigra intus albidae, structura firma compacta solida, cunctae prima aetate dimidiatae hiantes, nonnullae quoad formam regulares, ceterae tandem confluenti difformes in plagas rugosas congestae. Asci erecti adfixi paraphysophori; sporulae subglobosae uniseriales.

As has been pointed out by Bisby (1923), this change in classification came at the time when microscopical examination was beginning to have a place in the study of fungi, but internal microscopic characters were as yet almost unknown. As a consequence, the characterization of this genus, as of all other genera then recognized, was based largely upon macroscopic characters. It is noteworthy that, so far as internal characteristics are concerned, Chevallier's descriptions do not go farther than to state that there are present 'erect asci fixed among paraphyses' and that the spores are 'minute, subglobose, undivided, and uniseriate.'

Chevallier appears to have followed the treatment of Fries (1823) in the delineation of Lophium and Hysterium; but in describing both Lophodermium and Schizoderma he is much less specific concerning internal structure. For Lophodermium he gives the following description:

Perithecium innato-prominulum solidum epidermide concretum nigrum, rima longitudinali suboblitterata aut in cristam degenerante. Asci erecti fixi. Species epiphytae Phacidiorum consortes.

while for Schizoderma no mention is made of either asci or spores.

With the present point of view, it is impossible to identify any except type material with complete assurance that it coincides with the original description. Nine species were included in Chevallier's treatment. Most of these have been removed since to other genera. But in the case of the first named species, *L. arundinaceum,* sufficient citations were given to make it possible to trace the history of the genus and its species previous to the time of Chevallier. It is, however, impossible to establish the species upon the modern basis of a historically accurate type specimen. The characterization as given by Chevallier follows:

L. arundinaceum N. parvum ovale vix prominulum submaculaeforme atrum, rima conspicua. Schrad. Journ. Bot. 2, t. 3, fig. 3. Fries. Syst. mycol. 2, p. .590.

Moug. et Nestl. Stirp. Crypt. no. 655. Hypoderma arundinaceum. D.C. Fl. fr. suppl. no. 825.

On trouve cette espece sur les tiges seches de l'Arundo phragmites. Ses peritheciums sont nombreus, ordinairement distincts, a peine proeminens, sous forme de petites taches, noires, pourvues d'une fente lineaire.

It is noteworthy that this segregation was actually the third to involve this species. It was described originally by Schrader in 1799 as Hysterium; but De Candolle in 1815 established the genus Hypoderma for subepidermal Hysteria and transferred to it this and four other species of Hysterium. Rebentisch (1804, p. 342) transferred the species again to Xyloma. But Fries in 1823 did not recognize the segregation proposed by De Candolle and returned all species to Hysterium. Chevallier, in 1822, had published his *"Essai sur les Hypoxylons Lichenoides"* and, in this, had revived De Candolle's genus Hypoderma but had, at the same time, removed from it three species, among the three, *H. arundinaceum,* which he transferred to his new genus Lophoderma. In 1826 he redescribed this genus, spelling the name on this occasion Lophodermium; and from this publication date the genus is commonly said to have been established.

The first species named by Chevallier is *L. arundinaceum,* which is therefore to be regarded as the type species of the genus. The other species included in Lophodermium by Chevallier were *L. gramineum, L. nervisequium, L. pinastri, L. petiolare, L. scirpinum, L. Rubi, L. herbarum,* and *L. xylomoides.* Certain of these have since been segregated into newer genera.

In his definition of Lophodermium Chevallier appears to have taken into account only macroscopic characters, with the single exception of the statement *"asci erecti fixi."* His description of the including order requires paraphyses and minute, subglobose, undivided spores,—characters repeated for the genera Lophium and Hysterium but not for Schizoderma. It might be assumed that similar characters would be expected in Lophodermium, unless the omission of a definite statement is to be taken as acknowledgment of Chevallier's probable failure to see and understand these structures. It is, at least, evident that in his treatment of the other genera he followed faithfully the characterizations given by Fries.

This point, however, was cleared up by De Notaris (1847). He defined Lophodermium on the present basis, as having filiform spores, and transferred to his revived De Candollian genus Hypoderma such of Chevallier's species as did not possess spores of this type. With the exception of the studies of von Höhnel (1917), which are to be discussed more fully later, there have been no significant changes in the concept of the genus up to the present time. The work of Rehm (1886, 1887) and of Lindau (1896) represent merely an elaboration of species numbers,

following the definitions laid down by De Notaris. Even the most recent workers, as Hilitzer (1929) and Darker (1932), have preferred the older concept, as elaborated by Rehm and Lindau, to the newer concepts of von Höhnel, which in this case as in many others has been regarded as entirely too fragmentary and radical for practical use. Hilitzer, however, recognized the need of a new taxonomic placement of this and related genera. He also, while retaining the older concept, subdivided Lophodermium into a number of subgenera: Nervisequia, for species following the nerves of needles of coniferous hosts; Pinastriformia, for deep-seated pine-inhabiting species; Petiolicola, for the single species reported to inhabit the petioles of dicotyledonous hosts; Hysterioidea, for the large number of Hysterium-like species on the blades of leaves of dicotyledons; and Arundinacea, for the large group of species and forms inhabiting the leaves, sheaths, and stems of grasses and sedges. Certain other of the 40 species considered by Hilitzer, both on monocotyledonous and dicotyledonous hosts, were left unsegregated in these subgenera.

Darker's (1932) treatment relates only to species inhabiting conifers, and in dealing with these he has recognized, after the example of Dearness (1924), some of the more modern tendencies, such as the segregation of some species, *e.g., L. nervisequium* Chev., *L. montivaga Petrak,* into von Tubeuf's (1895) genus Hypodermella and of others into von Höhnel's (1917) genus Bifusella.

In the present treatment, these segregations have been recognized, for the reason that they at least serve to simplify Lophodermium by reducing both the number and the complexity of the array of species. While extreme forms are readily recognizable, the prime difficulty in following these changes in the practical identification of specimens is that the genera concerned have been set apart with such variations as length and shape of the spore as primary characters—characters which, in some of their manifestations, are scarcely distinguishable from the formal characters of the original genus. Nevertheless, the species treated in the body of this paper are those that have not been satisfactorily deposited in these newer genera.

MORPHOLOGY

1. GENERAL FEATURES

LOPHODERMIUM, as has been indicated in the historical section, is an Ascomycete the asci of which are contained in an elongated ascoma such as that illustrated in Plate I, Fig. 1. This structure is immersed in the host tissue and opens by means of a median longitudinal slit. The hymenium arises on the base of the ascoma and consists of subcylindrical

asci and filameritous, unbranched paraphyses. The asci contain, as a rule, 8 hyaline, nonseptate, filamentous spores.

THE HYSTEROTHECIUM.—The ascoma is generally known under the name hysterothecium, a term coined by Clements (1909) in order to distinguish between ascomata of this type (which he seems to regard as elongated perithecia with correspondingly elongated ostioles) and apothecia in which the opening takes the form of irregularly radiate cracks or a complete breaking away in an irregular fashion of a larger or smaller portion of the cover.

In Lophodermium, the hysterothecium is in all typical cases longer than broad. There is, however, much variation. In some species it is very broadly oval and may approach a circular form, while in others its length is so great in proportion to its width that its general form is best described as linear. To the unaided eye hysterothecia appear as tiny black spots on the host, sometimes shiny but usually dull, and mostly less than 1 mm. long.

The shapes of the ends of the hysterothecium vary to some extent, more particularly as between species than as between representative samples of a species; and they can be described with some accuracy as being truncate, sharply or bluntly rounded, or apiculate.

Under moderate magnification (12 × for most species, up to 30 × for the tiniest) the slit can be clearly seen. It seldom extends the entire length of the hysterothecium and is bordered on each side by heavy labia, which spread apart and reveal the hymenium to varying degrees. These labia vary in distinctness, in width, in length with relation to the hysterothecium, in degree of carbonization, and in thickness. It is distinctive of them, however, that they form a definite linear structure very similar to a true ostiole; and they are to be regarded as a definite provision for the emission of spores. The hygroscopic characteristic usually attributed to them probably does not exist in most species. The split occurs, not as a result of the swelling attendant upon absorption of moisture but as a result of the normal growth and development of attendant structures. Normally the lips completely inclose the slit; but in some species, and often in old specimens, cracking of the cover along the line of the split occurs beyond the lips at one or both ends of the hysterothecium and gives the appearance of a structure less definite than is actually present.

Darker (1932) has called attention to the occurrence in some species, *e.g.*, in *L. juniperinum* and *L. pinastri,* of rows of hyaline, papillate cells along the inner edges of the lips. These he describes as dove-tailing into one another. This structure seems to have been described on the basis of a misconception. Either it forms no part of the hysterothecium proper, in which case it is merely the cuticle or epidermis of the host, or it is the dried remains of the opening mechanism.

In section, the hysterothecium appears somewhat applanate and lenticular to triangular, as illustrated in Plate I, Figs. 2 and 3. It consists of a basal layer, variable in thickness according to species, composed of pseudoparenchymatous, brown cells. Above this is a layer of hyaline plectenchyma, in which there is often a definitely evident columnar arrangement of cells. This layer also is variable in thickness, both according to species and age of specimen. Because it is the layer from which the hymenium appears to arise, it has been termed the hypothecium by Hilitzer (1929). Covering the hymenium is a layer of more or less carbonized tissue, evidently distinct at the edges from the basal layer, variable in thickness according to species, composed of pseudoparenchymatous cells thickened or carbonized so as to resemble collenchyma tissue in higher plants. Hilitzer (1929) has used the term "melenchyma" to describe this and also the thick basal tissue of certain species, but the author will use in subsequent pages the term "pseudocollenchyma" as more suitable and perhaps more accurately descriptive of the aspect of the tissue, though it will be understood that he does not imply any similarity of origin between this and the collenchyma of higher plants.

In the median region of the hysterothecial cover, a very heavy carbonization usually takes place, making it impossible, even in the thinnest sections, to distinguish clearly the cell structure; but a longitudinal band of cells, such as those shown in Plate I, Fig. 3, remains less carbonized and separates the carbonized region longitudinally into the halves which eventually form the labia of the hysterothecium.

In mature material, the lips are bordered inwardly, Plate I, Figs. 1, 2, 4, 5, by a layer of gelatinized, short filaments which are homologous with the periphyses of the Sphaeriales.

THE HYMENIUM.—Most of the interior of the hysterothecium is occupied by the hymenium. This consists of erect, intermixed asci and paraphyses. Both the asci and the paraphyses arise from a hyaline, subhymenial plectenchyma of very fine hyphae whose intricate interweaving conceals the method of ascus formation. In most forms the paraphyses exceed the asci in length, and their overtopping portions, becoming gelatinously agglutinated, form a dense layer, readily visible through the hysterothecial slit, which has been quite generally called the epithecium. In most species the epithecium shows as a silvery white layer; but in a few species it is brilliantly tinted, the tints varying with the species and ranging from yellow to deep orange.

The hymenium arises only from the morphological base of the hysterothecium and does not, in any species examined by the writer (though it has been so described by others), extend upward along the sides, *i.e.*, the cover, of the hysterothecium.

THE ASCUS.—The asci, in accord with the shape of the spores, are much longer than wide. the ratio of width to length varies between species but is usually as from 1/10 to 1/15. The general shape varies from clavate to cylindrical, much variation occurring within a given species, or indeed among the asci in a single hysterothecium. It is difficult to describe the asci accurately. At the apex, they are asymmetrical, more or less conical, and rounded to subacute when viewed from one side; but a view at right angles to this reveals only a symmetrically rounded or subacute form. This is apparently due to an arrangement of the spores which is described later. In some species the asci have been described as having rostrate apices, reference being made, thereby, to the tendency of the ascus to conform closely, when wet, to the shape and arrangement of the swollen spores. The ascus is almost invariably widest at or above the middle. Below this point, according to species, and often with much variation within a single hysterothecium, its inclosing walls taper to a broad or a fine foot, leaving little or much of the basal part of the ascus unoccupied with spores. Almost uniformly, the asci contain 8 spores.

ASCOSPORES.—The ascospores are hyaline, nonseptate, filamentous, and of practically uniform diameter throughout. Length, with some variation among species, tends to approach that of the ascus and is very great in proportion to the diameter. In many species the ascospores are incased in a conspicuous hyaline, gelatinous matrix which varies in thickness according to the species. This matrix is probably present in all species, but in those species with very narrow asci and spores it is indistinct and seems in ordinary miscroscopic mounts to be absent. Its presence can usually be demonstrated, however, by heating the slide with a little lactic acid added to the mount.

The arrangement of the ascospores within the ascus is a character that has not received much attention. Being linear, the spores reach from the apex to near the stipe of the ascus and lie parallel with each other. The term "fasciculate" has been used to designate this condition. Besides being fasciculate, the spores are arranged very definitely in pairs, as shown in Plate I, Fig. 6. Such an arrangement is what might be expected in the light of Dodge's (1931) recent investigation of ascospore formation. The individuals of each pair of spores lie parallel with each other, and the pairs are arranged in a series of four. One pair terminates just at the tip of the ascus; a second pair lies immediately to the front of the first and somewhat lower in the ascus, and the succeeding 2 pairs of the series are similarly stepped forward and downward. It is this ranked arrangement of the ascospores that gives to the ascus, in a lateral view, its asymmetrically conical apex.

In many species there is a marked tendency for the spores to be twisted or coiled in the ascus. In general, this is slight and may in fact be due to twisting of the ascus in its growth. In a few species, however, the twisting of the spores is very pronounced, as shown in Plate I, Fig. 7; and in these cases they assume intricately coiled positions with the distal and usually the basal portions nevertheless straight and definitely indicative of the pairs.

Darker (1932) has pointed out that there is little variation in length of spore due to drying, but that dessication very markedly influences spore width. Prolonged soaking in water tends to restore dried spores and asci to their natural diameter; and for quick microscopical examination the same end can be achieved by heating in a 3 per cent aqueous potassium hydroxide solution.

PARAPHYSES.—These structures arise in most species from a series of columnar cells which form the top of the subhymenial plectenchyma. They are hyaline, filamentous, nonseptate, and normally unbranched. In the case of many species, they have been described as coiled, bent, or hooked at the apex (Hilitzer, 1929, fig. 7). This variation in their apices appears, however, to have been subject to much misinterpretation. In the examination of many specimens of many species, I have seen no case in which the tips of the paraphyses could be accurately described as coiled. As a matter of fact such an appearance, readily misinterpreted with improperly prepared slides under low magnifications, is invariably the result of pressure against the hysterothecial cover by which the tips are irregularly bent or crushed. The degree to which the bending and crushing occurs is determined, evidently, by the position of the individual paraphysis in the hysterothecium and by the direction it is forced to take prior to the opening of the hysterothecium. The frequently described uncinate, or hooked, paraphysis tip is likewise largely the result of misinterpretation. *L. uncinatum* Darker is the only species in which I have found definitely hooked paraphysis tips, and their occurrence even in this species appears, upon careful examination, to be limited to the extreme sides of the hysterothecium, suggesting again the formative effect of pressure against the cover.

A variable, but often distinctly observable characteristic of paraphyses is that their distal ends are clavately expanded, as shown in Plate I, Fig. 6. The degree to which this occurs, or its entire absence, constitutes one of the characters, describable with difficulty, by which a species may be recognized.

2. PARTICULAR FEATURES

IN ADDITION to these general characters of the genus, there are certain particular features of morphology that deserve special mention. According to the structures to which they appertain, they are given below.

HYSTEROTHECIUM.—In addition to the general structure described in the preceding section, true of all species hitherto classed as Lophodermia, there are certain more intimate details which will now be recognized as of exceptional importance. These include: (A) the position of the hysterothecium with respect to host tissues; (B) mycelial structure of the hysterothecium; (C) general structure of the hysterothecium; and (D) the nature of the slit.

(A) *Position in the Host Tissue.*—This character, as has been pointed out previously, is not entirely of recent recognition. Prior to the segregation of filiform-spored species, De Candole (1815) segregated in his genus Hypoderma those species of Hysterium having hysterothecia situated subepidermally. With the development by Corda (1842), De Notaris (1847), and Duby (1861) of spore characters as a means of delimiting genera, the significance of the situations of the hysterothecia with respect to the tissues of the host was over shadowed and almost entirely dropped from sight. It was not again revived until von Höhnel published his studies of the Phacidiales in 1917; and his revival of this characteristic must be attributed to the use of it by Theissen and Sydow (1915) in their monographic studies of the Phyllachoraceae. In von Höhnel's treatment, he based the division of the Phacidiales into families upon the position of the ascocarp or ascoma in the host tissue and used as characters for genera the nature of the stroma and the shape and segmentation of the spores.

For various species of Lophodermium, this procedure resulted in a segregation into entirely new families and genera. While it has generally been regarded as radically untenable, it is, in the writer's opinion, the first real contribution to the classification of Hypodermataceae and related forms since the work of Duby in 1861. Unfortunately, even recent workers have failed to see its significance, Darker (1932) recognizing this character only to the extent of employing it as a means of distinguishing species.

Within the genus Lophodermium, as understood by Rehm and Lindau, it seems characteristic of certain species that they are oriented within the host very definitely with respect to the host tissues. Certain species, *e.g.*, *L. arundinaceum* and *L. pinastri* (*sensu* Darker, 1932), the hysterothecium is definitely placed deep in the host tissue, *i.e.*, it develops and lies at maturity beneath the epidermis; other species, as *L. Piceae* (*sensu* von Höhnel) are developed within the epidermal layer, actually separating the epidermal cells in halves and occupying at maturity the space thus made; and still other species, as *L. nitens* and *L. juniperinum,* are developed beneath the cuticle of the host. For these, according to the

scheme of von Höhnel, genera have been created and these genera segregated into families, the prime characteristic of which is the location of the ascus-bearing structure.

The determination of the position of the fruiting structure in the host has been subject to misinterpretation. Whether or not the fungi concerned are parasitic, it is a fact that their presence results in much destruction of the internal tissues of their host, regardless of the position of the fruiting structures, and in many cases the only parts of the host left intact are the two epidermises. The tissues intervening are almost completely disorganized and the space is occupied by the internal mycelium of the fungus. Pressure exerted during the formation of the hysterothecium naturally tends to force the basal portion of it more or less deeply into the host, with the result that, in a superficial examination, even such species as are strictly subcuticular appear to lie below the epidermis. If carefully examined at the margins of the hysterothecia, however, where the host tissue is usually still intact, the true level of insertion can always be determined; and this can be substantiated by determining what tissues lie above or are involved in the formation or the construction of the hysterothecial cover. It is important, therefore, in determining the position of the fruiting structure, to take into account not the apparent situation of the body of the entire mature hysterothecium but the depth at which the margins of the hysterothecia are inserted and the particular tissues overlying it in the regions of the cover. The three positions of the hysterothecia of Lophodermium are illustrated in Plate I, Figs. 2, 3, and 4.

In certain of the hosts attacked by species of Lophodermium, especially Pinus, Picea, and many grasses, there exists beneath the epidermis a series of lignified cells called hypodermis. These are, morphologically, transformed mesophyll cells. Subepidermal species of Lophodermium make no distinction between hypodermal cells and other mesophyll; and there is no significance to be attached to the fact that in some species a few of these cells, either wholly or in part, become fabricated with the cover of the hysterothecium. This is illustrated especially by *L. arundinaceum*, in which the remains of hypodermal cells are to be found incorporated in both the cover and the base of the hysterothecium, when they are not completely disintegrated.

(B) *Mycelial Composition of the Hysterothecium.*—As illustrated in Plate I, Figs. 2, 3, and 4, the hysterothecium in section appears to be composed of layers of more or less carbonized, pseudoparenchymatous fungous cells. When carbonization is only partially attained, heavy darkening of the cell walls occurs at certain points only, giving an aspect very suggestive (though only on a very small scale) of the collenchyma cells encountered in higher plants (Plate I, Fig. 8). The relative thick-

ness of the pseudoparenchyma, both in the base and in the cover, though variable, may often be characteristic of a species.

Beyond this point, similarity among the groups of species ceases. Those that are subepidermal and some that are intraepidermal appear to be composed throughout of pseudoparenchymatous cells. But those that are subcuticular and some that are intraepidermal have in addition to the mass of pseudoparenchymatous cells a definite external plate, and usually also an internal plate forming the base, either composed of or resulting from the growth of aliform mycelium. These plates (see Plate I, Fig. 8) are never more than one cell thick, and form a compact layer, usually brown, chytinized only along the sides of the strands in the cover, and not chytinized in the base, and of quite variable aspect, ranging from a meandering type to radiate forms very suggestive of microthyriaceous fungi.

These aliform plates are of radial development. In the young hysterothecia a number of central cells, often not more than 2 or 3, are to be found, both in the cover and the base. From these there develop, in an outward direction, closely adjacent hyphae which branch in a more or less typically aliform or dichotomous manner as they advance. The less typical branching gives rise to the plates made up of meandering cells (Plate I, Fig. 9), while the more typically aliform branching gives rise to those plates which most nearly resemble the mycelium found in the Microthyriaceae.

The degree to which the aliform cover and basal plates are developed differs among species, and the readiness with which their presence may be determined also varies. In intraepidermal species, the entire cover, and for the most part the basal layer also, appears to consist of more or less radially arranged lines or rows of pseudoparenchymatous cells, and their aliform derivation is determinable only by examining with care their outermost, marginal cells. These will, as a rule, be found to show, in their "mitten-shaped" outlines, their aliform manner of growth. In subcuticular species, both the cover plate and the basal plate are definitely aliform and easily observable to be so throughout the hysteriothecium, except in the region occupied by the heavily carbonized lips. In some species, as *L. nitens*, the aliform cover plate often extends outward beneath the cuticle as a compact, thin skirt to a considerable distance beyond the hysteriothecial pseudoparenchyma.

Pseudoparenchyma and its subcarbonized derivative, pseudocollenchyma, are evidently developed as inward proliferations from the basal and covering aliform plates.

(C) *General Structure of the Hysterothecium.*—As has been noted, the aliform plates of the cover and base originate from centrally placed

cells, those of the cover being distinct from those of the base. The two plates develop separately; but almost *pari-passu*. In the subcuticular and intraepidermal species, the cover and base plates are distinct and separate structures, between which the pseudoparenchyma, subhymenial layer, and hymenium are subsequently developed. The hysterothecium should be regarded not as a unit structure comparable to, and derived from fundamental cells in the same manner as are, the perithecia of the Sphaeriales but rather as of the type found in the Stigmateacea of the Hemisphaeriales, from which they differ distinctly in that they possess both base and cover.

While there is no aliform structure evident in the hysterothecia of subepidermal species, there is to be seen, when careful sections are prepared, a very evident distinction between base and cover (Plate I, Figs. 2 and 10). In fact, the separation between base and cover is just as distinct, often times more so, as in those species possessing aliform structure.

(D) *Nature of the Slit.*—It has been generally supposed that in Lophodermium the hysteriothecium opens by splitting longitudinally along a thin band of subcarbonized cells lying between two narrow, heavily carbonized, much thickened lips. The band of cells along which the split occurs was recognized by von Höhnel (1917) and by Hilitzer (1929), and was named "slit band" by Darker (1932).

When the covers of immature hysterothecia are viewed microscopically with transmitted light, the slit band appears as a ribbon of cells, of varying width, lying between and much more translucent than the labia. In sections (Plate I, Fig. 3), this band appears to be made up of pseudoparenchymatous cells differing in two respects from the remainder of the cover. In the first place, they are, though brown, not to any appreciable degree carbonized. In the second, they often appear more elongate and seem to lie rather definitely in vertical rows so as to give a columnar, or palisade, arrangement.

As a result of the subsequent development of the hystёrothecia, it seems evident that another characteristic of the slit band cells is that they have not lost their meristematic quality. It seems evident that, as the hysterothecium becomes mature, the opening develops, not as a result entirely of mechanical pressure, with the fissure occurring in the line marked by these weak-walled cells, but as the result of the development from this band of meristematic cells of numerous short filaments comparable in all respects to the ostiolar periphyses of the Sphaeriales. A cross section of the opening of the hysterothecium of *L. arundinaceum* is shown in Plate II, Fig. 1, with the position, relative size, and composition of these periphyses in detail.

The labia of all species of Lophodermium are lined inwardly, when

the hysterothecia are just recently opened, with a band of these peri-physes. Shortly after the opening of the hysterothecium, the band of peri-physes becomes more or less definitely gelatinized; and in many species it deliquesces rapidly and is lost quickly. In other species, however, *e.g., L. apiculatum,* and *L. melaleucum,* the periphyses are very persistent and, even in old and long-emptied hysterothecia, form a conspicuous silvery white crest upon the extraverted, cracked, and torn labia. In color they correspond with the epithecium, being in certain species, *e.g., L. melaleu-cum,* brilliantly tinted with yellow or orange.

MYCELIUM.—In the species of Lophodermium, as in most ascomy-cetes, there are few, if any, distinctive characteristics to be found in the mycelium. The parasitism of most species has been regarded as question-able, due presumably to the fact that practically all species growing on conifers and grasses, and many of those growing on dicotyledonous sub-strata, do not develop hysterothecia until the leaves upon which they are formed have been shed by the plant and have been upon the ground for a considerable period of time. Nevertheless, certain adaptations to host structure are evident in various classes of species.

It is noteworthy, for example, that the attack of the fungus, in nearly all cases, causes changes within the host which result in the formation of spots. These spots are usually stramineous, extensive, and irregular in shape. In graminicole species, it is characteristic that the spots, though not sharply delineated from the surrounding decomposed tissue, present a cleaner, more preserved appearance.

In the pinicole species, it is characteristic of the spots that they are sharply delimited by definite black lines, along which the needles break very easily. Those needles which are attacked at several points have the individual areas of infections sharply delimited from one another by these black lines, and under the microscope it is readily seen that the black line which separates two adjacent spots is, in fact, a double line. The limiting line of one infection is separated from the limiting line of the other in-fection by a small band of unoccupied host tissue. In microtome sections, these black lines are found to exist not merely on the surface of the host organ but to extend as a plate, or layer, through the entire section of the needle. They are composed of closely interwoven, often compacted, pseudoparenchymatic, carbonized strands of mycelium. The formation of the double lines by adjacent infections may perhaps be regarded as an antibiotic reaction.

In species inhabiting dicotyledonous hosts, infection spots are also, for the most part, sharply delimited by the formation of black stromatic mycelial structures. These do not, however, exhibit the same sharp antibiotic reactions that are seen in pinicole species. Adjacent spots may

merge and in subsequent development become considerably overlapped; and when the development of the fungus in one has ceased, its black delimitation will be found to have been laid down with reference only to itself, traversing the spot it overlaps and crossing, at the margin, the stomatic line of the overlapped spot.

Subepidermal species characteristically produce only internal mycelium. This is fine, hyaline, and septate, and ramifies through the host tissue, destroying particularly the mesophyll and causing collapse of the epidermal layers. There is left, then, only a leaf skeleton, composed of upper and lower epidermis and partially disintegrated veins and veinlets. This internal mycelium is very fine, usually less than 2 μ in diameter, and hyaline. About the bases of the hysterothecia it collects in closely interwoven hyaline mats resembling internal subicles (Plate I, Figs. 2 and 4), and was regarded by Miles (1926) as a part of an internal dothideaceous stromatic structure.

Subcuticular species, and occasionally others, have in addition to the internal hyaline mycelium a subcuticular or intraepidermal coarse, brown, distantly septate mycelium that is intimately connected with the covers of the hysterothecia (Plate II, Fig. 5.) When well developed, as in *L. melaleucum*, it has the appearance of a network, due to its frequent branching and the tendency of the hyphal threads to follow the lines of union of the epidermal cells. In some forms there is a tendency for this extra-hysterothecial mycelium to become aliform, that is, it often divides dichotomously, and some of the tips of the strands bear the mitten-shaped terminal cells characteristic of such mycelium. There is not, however, any indication of the presence of hyphopodia or hophopodium-like organs.

Intraepidermal species are less destructive of the host tissue. For the most part, mesophyll cells are not disintegrated; but the internal hyaline mycelium penetrates at will throughout the mesophyll, occupying both the intercellular spaces and the intracellular cavities. Material used for food by these species is evidently limited rather definitely to the material laid down by the host as secondary and tertiary thickenings of its cell walls. It is notable, also, that in these species there exists a coarser, usually brown mycelium, similar to the subcuticular mycelium of the subcuticular species, which invades and traverses the epidermal cells. It may more or less compactly fill the epidermal cells lying at the end of the hysterothecia; and when it straggles out into more distant host cells there is often an indication of its aliform nature to be found in the mitten-shaped terminations of individual hyphae.

PYCNIDIAL FORMS.—Imperfect or conidial forms have been observed in close association with the hysterothecia of Lophodermium and other hysteroid fungi by many observers. Their significance in the life history

of the fungi to which they are said to belong has been little understood. Actual connection has been difficult to prove; but their constant occurrence and obviously close connection with the hysterothecial stages seems to substantiate their relationship. They are for the most part, if not without exception, assignable to genera of the Fungi Imperfecti usually considered as members of the Leptostromataceae. Practice in designating them has varied. Rehm (1887), Lindau (1896), and others have simply included their names, when they have been named, in the synonomy of the perfect stage and have given descriptions of the spore forms as a part of the description of the species. Hilitzer (1929), on the other hand, has established new Imperfect genera and species for the Imperfect spore forms and has given their descriptions as separate entities, while designating them as the imperfect forms of the species to which they are thought to belong.

It appears that, without exception, these Imperfect forms are situated with relation to the host tissues in exact correspondence with the hysterothecia to which they are related, and their mycelial structure is also in agreement. The spores are, in most species, rod-shaped, hyaline and nonseptate; and the conidiophores are short, hyaline, and arranged in a basal layer. Dehiscence of the conidial structure appears to be irregular (though the complete morphology of the pycnidial forms has not been carefully studied); and this and the relative development of pycnidial tissue determine the generic assignment of the various forms.

SUB-STOMATAL SCLEROTIA.—In all pinicolous species of Lophodermium, and in many species inhabiting monocotyledons and dicotyledons, growth of the fungous mycelium within the host tissues is accompanied by the formation of heavy, carbonized masses of mycelium beneath stomatal openings (Plate II, Fig. 2). These structures have been variously interpreted. Hilitzer (1929) regards them, at least in part, as structures formed by the mycelium of the fungus immediately after penetration of the host. According to this view, they constitute a focus from which emanates the mycelium that makes up the individual infection. This interpretation has, as a draw-back, the fact that every spot, or colony, develops enormous numbers of these sclerotia, the number being limited, in fact, only by the number of stomata included within the area of host attacked. Killian and Likhité (1924) and Likhité (1926) regard them, at least in some cases, as the primordia within which the first process of fertilization takes place prior to the development of the hysterothecium. This may be, in part, true; but it cannot hold for all cases, else the number of hysterothecia in any infection would be so great that there would not be room for their full development.

DEVELOPMENT OF THE HYSTEROTHECIUM.—The period required from

the time when infection takes place until the final maturity of the hysterothecia has not been determined for many species. Those that have been followed are chiefly pinicole forms, and among them there is a very considerable variation in the time required. *Lophodermium laricinum* is known to be able to complete its development in one year (Darker, 1932), and certain species, *e.g., L. hysterioides* and *L. macularc,* which attack living leaves of deciduous dicotyledons, probably also require but one year. Most other species appear to require a longer time.

The process involved in the development of the hysterothecia, and of the asci and spores, has received less attention in this group than in any other group of ascomycetes. Killian and Likhité (1924) and Likhité (1926) have made the principal, and nearly the only, contributions.

In the case of *L. hysterioides,* a subcuticular species, it is reported that at the beginning of its development the hysterothecial stroma is strongly flattened, so that it is difficult to observe the ascogenous cells. There is in the interior of the sclerotial mass, however, one or more large, multinucleate cells with dense protoplasm which later give rise to a long chain of ascogonial cells, these numbering about 40 and having a size of 1.5–6 μ and their nuclei about 1–1.5 μ. These cells form a spiral, oriented in the plane of the stroma, *i.e.,* parallel with the surface of the leaf, and so are not readily distinguished in ordinary transverse sections.

The first cells produced—ascogonial mother cells—degenerate after the formation of the ascogonial cells, and at the same time the ascogonial cells increase in size, attaining diameters of 5 to 8 μ. This is followed by a partial absorption of the walls separating them, and it is probable, though not observed, that the nuclei migrate through these perforations to the cells at the summit of the spiral. It was observed, at least, that subsequently the summit cells of the spiral contained numerous nuclei.

Subsequently, the other cells degenerate and there appears an extensive development of hyphae which constitute the paraphyses. These arise from spherical cells with peripheral protoplasm and many nuclei. The growth of the paraphyses serves to elevate the hysterothecial cover and prepare the space necessary for the development of the asci.

Each ascogonial cell bears protuberances at its summit. Its nuclei undergo new divisions, becoming smaller and smaller. The protuberances, at the same time, elongate and become at length ascogenous hyphae; but the production of hook cells was not observed in connection with their growth.

The origin of the stroma in which these processes occur has also been described in some detail. The spore, after its germination on the lower face of the leaf, gives rise to a mycelium which enlarges little by little into a large membrane. This mycelium penetrates through stomatal open-

ings and, beneath the stomata, becomes transformed into sclerotial masses which clog the stomata. From there it spreads through the mesophyll. Much later, the substomatal sclerotia give rise to a special mycelium, more delicate than the other and very fine, which penetrates between the cuticle and the epidermis and there forms the stroma destined to become the hysterothecium.

This account by Likhité (1926) is in agreement, essentially, with the account given by Prilleux (1897) for *L. macrosporum;* but I have been unable to substantiate either account satisfactorily. It is undoubtedly true that the stomata and substomatal cavities become clogged with carbonized, sclerotia-like masses of cells (Plate II, Fig. 2) ; but this is true of all stomata ; and the masses appear to have arisen from, rather than to have given rise to, the internal mycelium. In material available to me, it has been apparent that hysterothecia arise independently of these substomatal masses, as the result of the laying down of a few cells from which the basal and covering layers develop independently by radial or subradial growth. Even in the most carefully prepared sections, and with excellent microscopic equipment at hand, it has been impossible for me to identify with anything like certainty the ascogonial mother cells (Plate IV, Fig. 4), ascogonial spirals, or ascogenous hyphae. While some such process as that described by Likhité undoubtedly occurs, the point at which it begins, its relation to the presence of an already forming hysterothecium, and the nuclear, as well as many of the anatomical, details need much closer investigation.

TAXONOMIC RELATIONSHIPS

1. Present Status

The changes that have occurred in the classification of species of Lophodermium have been given in some detail in the historical section. Segregation of species and the grouping of them into genera, as well as the placement of the genera in families and orders, has been based from the beginning on a few superficial characters of the hysterothecium, supplemented in later years by spore shape and septation.

Fries (1823) included all species then known in Tode's genus Hysterium. Two outstanding distinctions, namely, the elliptical or elongated ascocarp and dehiscence by a simple longitudinal slit, separated this genus from others placed in the family Phacidiacei. This family was one of three constituting the order Pyrenomycetes and was distinguished by the perithecia becoming at length erumpent and by possessing an exposed or open disc. In contrast, the family Sphaeriacei was characterized as having closed perithecia perforated by an ostiole and the family Xylomacei as having obsolete asci and innate spores.

The Pyrenomycetes constituted, according to Fries' views, the second of five orders included in the second class of fungi, which he termed the Gasteromycetes. This class was intended to include bladder-like fungi composed of cells united into a form tending to become rotund and closed at first but opening either by means of a definitely formed ostiole or by irregular breaking. The Pyrenomycetes were distinguished by having bladder-like fruiting structures in the form of receptacles or chambers and spores collected in series in asci.

The concept of the Pyrenomycetes has persisted; but many subsequent modifications in classification have tended to give the term "pyrenomycete" a general rather than a specific meaning, and its use is now limited to the gross visual aspect of fungi. It does not imply the presence of any taxonomically significant anatomical character.

Chief among the modifications of Fries' original system of classification, so far as they apply to Lophodermium, are the following.

Chevallier (1826) separated hysteriaceous from phacidiaceous forms and gave his class Cheilomyci, which contained the former, equal rank with his Phacomyci, which contained the latter.

Fries (1835) brought together in a group all ascomycetes with hymenia exposed at maturity and these he designated as Discomycetes. In this group, he included the Phacidiacei of his earlier publication.

Corda (1842) proposed the order Hysteriaceae (Hysteriales in present terminology), but in contrast with Fries included in it the Phacidiacei. Corda's exceptional contribution was, however, the introduction of spore characters as criteria in delimiting genera.

De Notaris (1847) developed the use of spore characters to a still greater extent, dividing the Hysteriacei into Phaeosporii and Hyalosporii on the basis of spore color.

Duby (1861), while still regarding the Hysterineae as a group belonging to the Pyrenomycetes, made a primary separation on the shape of the ascomata, naming those which possess erect, laterally compressed receptacles Lophiees and those which possess flattened receptacles Hysteriees.

Rehm (1886), in his revision of the Hysteriales in the Duby herbarium, and later (1887) in Rabenhorst's Kryptogamen-Flora, brought forward the classification that has received general acceptance, even by such recent students as Hilitzer (1929) and Darker (1932). He regarded the group as a distinct order and considered it as forming a connection between the Pyrenomycetes and the Discomycetes. Toward the first, relationship was held to be shown especially by the elongated opening of the fruiting structure, the connection being with the Lophiostomeae, while toward the second, relationship was held to lie in the elongated form of

the ascoma and the apothecium-like method of dehiscence, which appears to have been regarded merely as mechanical breaking.

Lindau (1896) brought Rehm's system into conformity with modern terminology and united Rhem's distinctions between genera with those developed by Spegazzini (1880) and Saccardo (1883) on the basis of spore characters into the present system of classification.

Throughout the work of these mycologists, there has been a persistent tendency to regard the gross form of the mature hysterothecium as the criterion upon which the interpretation of taxonomic relationship should be based. The individual characters to which taxonomic significance has been attributed may be cataloged as follows:

(1) *Spores are borne in asci.* This is of general significance only, and places species as ascomycetes.

(2) *Asci are contained in a receptacle.* This also is of general significance, placing species among the large group of Euascomycetes having definitely constructed ascus containers.

(3) *The asci are grouped, erect, among paraphyses, in a well-defined layer termed the hymenium.* This serves to distinguish these fungi from those having the asci placed in various positions, as in the Aspergillales and Myriangiales.

(4) *The hymenium forms a basal disc in the receptacle.* This character is interpreted as showing relationship with Discomycetes.

(5) *The receptacle, closed at first, opens eventually by mechanical breakage.* This has been held to be a primitive combination, indicating relationship with phacidiaceous forms.

(6) *The opening of the hysterothecium is a longitudinal slit bordered by thick labia.* In this character, similarity with the complete perithecia of the Lophiostomataceae, which have elongated, laterally compressed ostioles, is observed. Progression toward, or relationship with, the Sphaeriales is thought to be indicated.

In their sum, these considerations lead to the expression by Gäumann (1928, Dodge's translation): "With the Hysteriales begins the group of hemiangiocarpous Ascomycetes; they are Pyrenomycetes with elongate perithecia, closed during development, opening at maturity by a long slit which follows an earlier dehiscence line and almost completely uncovering the hymenium."

At present, the order Hysteriales is constituted of five families. These are grouped primarily according to the connection that exists between the ascocarp and the host tissue. Two families, the Hysteriaceae and Acrospermaceae, develop their ascocarps free of the host tissue. Three families, the Hypodermataceae, Dichenaceae, and Ostropaceae, develop ascocarps which are at first immersed in the host tissue but which become erumpent. The Hypodermataceae are distinguished, in their turn, by having the walls of the ascocarps connate with the host tissue.

Within the Hypodermataceae, Lophodermium is at present set apart as a genus almost entirely upon ascus and spore characters. These are (1) asci that are essentially cylindrical in shape, rather than clavate, and

(2) ascospores that are 1-celled, filiform, and essentially of uniform diameter.

In contrast with the line of taxonomic development just summarized, von Höhnel (1918) has proposed that certain genera now included in the Lophiostomataceae and many genera of the Hysteriales should, because of the elongated perithecial opening common to both, be united in a new order, for which he has proposed the name Hysterostomeae. This does not, however, affect any species of Lophodermium. Prior to this (1917), however, he brought together certain genera of the Phacidiaceae and of the Hypodermataceae, including a number of species of Lophodermium, and constructed from them the skeleton of an order which he designated the Phacidiales. This name must be taken in a sense much different from its usual interpretation, for von Höhnel states that he considers it a connecting order between the Dothidiales and the Pezizales.

Within this order, according to von Höhnel's conception, families are distinguished by a single character, namely, the position of the ascocarp with respect to the host tissues. When the ascocarp is entirely external, *i.e.*, seated on the cuticle, membership in the Schizothyrieen is indicated; when it is situated between cuticle and epidermis, membership is in the Leptopeltineen; when within the epidermis, membership is in the Dermopeltineen; and when beneath the epidermis or deeper in the host tissue, in the Phacidiaceen. Further distinctions are made that do not involve any species of Lophodermium.

Within each of these families, genera are distinguished primarily upon the presence or absence of a stroma, secondarily upon spore form and septation, and finally upon the type of opening exhibited by the ascocarp.

The species of Lophodermium, though usually considered to be united by the common absence of a stroma, by the possession of filiform, nonseptate spores, and by an elongated hysterothecial opening, fall among three of von Höhnel's families, according to their position with relation to the host tissues. *Lophodermium arundinaceum* is a member of the Phacidiaceen; and, since it is the type species and retains the generic name, new genera are named by von Höhnel to contain the species falling in other families. The intraepidermal *Lophodermium hysterioides* is renamed *Lophodermellina hysterioides* in the Dermopeltineen, and the subcuticular *Lophodermium melaleucum* is renamed *Lophodermina melaleuca* in the Leptopeltineen.

The treatment given by von Höhnel was limited to exemplary species, and the majority of species included in Lophodermium have never been transferred, formally, to the positions they would occupy in his system.

In this rearrangement there is the advantage that the level of insertion of the ascocarp in the host tissues has been given consideration. Clements

and Shear (1931) recognize that the general position of the ascocarp with relation to the host tissue, *i.e.,* whether it is innate or superficial, affords a criterion of generic significance; but at the same time they express the opinion that to regard relative depth of insertion as equally important is to assume an extreme view. Admittedly, there is at present no means of weighing the relative values of criteria. But it would seem that the criterion of depth of insertion, if found reliable with regard to individual species in a large and heterogeneous genus, would furnish a satisfactorily practical method for grouping the species either into a number of genera or subgenera. To argue concerning the rank properly due such a criterion serves only to add confusion. The writer holds the opinion that, in systematizing the species of Lophodermium, the best separation can be made at the present time on a generic basis, as this criterion does not run completely parallel with either host relations or other lesser anatomical criteria.

2. NEW TAXONOMIC FACTORS

As a result of the development of microscopical equipment and technique, it would seem that a more satisfactory anatomical basis for classification than that outlined above might have been obtained; but the most recent students (Hilitzer, 1929; Darker, 1932), however much they may have observed, have deemed it desirable to present their work in the taxonomic pattern now accepted.

It is the writer's intention, therefore, to present here in a rather brief way such results of his studies as tend to suggest a basis for a more serviceable classification, when amplified to include other genera.

THE HYSTEROTHECIUM.—As is evident from the foregoing discussion, this structure has been regarded by various workers as either an apothecium or a perithecium. The term hysterothecium merely takes cognizance of the shape of the structure. Both of these views involve the basic idea that it is a unit structure; that is to say, if it is regarded as an apothecium its outer walls are, in ontogeny and at maturity, continuous from the middle of the base to the middle of the top, or if it is regarded as a perithecium the same conception of its structure must be admitted with the exception that the opening is to be regarded as a definitely developed ostiole rather than the result of mechanical stresses.

Vertical sections of hysterothecia, when taken either in longitudinal or transverse directions, do not support the conception of a hysterothecium as a unit structure. Instead, it is evident that a hysterothecium consists of two separate, distinct, and independently though simultaneously developed parts, the base and the cover.

In the case of *Lophodermium arundinaceum*, the type species of the genus, which is inserted subepidermally in its host, the separation between base and cover is very distinct. A longitudinal section taken near the middle of a mature hysterothecium is shown diagrammatically in Plate I, Fig. 10. The material from which the section was made is Mougeton et Nestler, *Stirp. Crypt. No. 655*, cited by both Fries (1823) and Chevallier (1826). At the two ends of the section, where continuity of tissue would be expected if the hysterothecium were a unit, an open gap appears between the two strata of pseudoparenchyma that form the cover and the base, and the gap is filled more or less completely by the same fine, hyaline plectenchyma that gives rise to the hymenium.

Nearly the same condition is apparent in Plate I, Fig. 2, in which a detailed cross section taken near the middle of a hysterothecium of the same species is shown. Here, however, the basal pseudoparenchyma extends outward at the margins and forms a flat rim upon which the edges of the cover rest.

Even under very high magnification, no connection between the two strata can be discerned; and the microscopical evidence is supported by the ease with which the cover can be removed intact from the base after material has been macerated chemically in a sodium hydroxide solution to loosen the host tissues.

In *Lophodermium pinastri* (*L. Piceae* von Höhnel) on Picea, a species uniformly developed within the epidermal zone, a similar independence of cover and base exists. Plate I, Fig. 3, shows a cross section taken from near the middle of an immature hysterothecium. The base had not yet become carbonized, but the cover appears to be fully carbonized. In the diagrammatic drawing, it appears that the cover extends outward, beyond the base, forming an inclosing lid.

The manner in which the two layers, cover and base, become differentiated, is shown in Plate II, Fig. 3. This figure is drawn from the margin, under oil immersion, of the same section shown in Plate I, Fig. 3. At the left of the figure, the epidermal cells of the host are filled with hyphal cells composing the hysterothecial margin. It should be noted that in each host cell there are just two rows, one above the other, of fungous cells. At the margins of young hysterothecia, these are compactly placed. But this compactness extends inward from the hysterothecial margin through only 2 or 3 epidermal cells. From that point inward, the two rows of cells begin to be separated, apparently forcibly by the elongation, vertically, of certain upper cells, which grow downward in the form of suspensors or props and raise the cover layer, providing room for the development of the hypothecium and hymenium.

In those species that are inserted between the cuticle and the epidermis, the top and the base are also distinct structures. Plate I, Fig. 4, shows in detail a cross section taken near the middle of a mature hysterothecium of *Lophodermium maculare*. In this species, the outermost layer of cells of the cover is distinctly aliform in structure and appears to develop by radiating growth. The figure shows how the aliform layer exceeds the basal layer of pseudoparenchyma at the margins, forming a cap slightly more extensive than the base which it covers. Plate I, Fig. 5, a section taken near one end of the same hysterothecium, shows more clearly the separation that exists at the margins between base and cover. That this separation is not merely an optical one resulting from differences in depth of cell coloration is shown when careful examination is made of the marginal region in thin sections under an oil immersion lens. Plate II, Fig. 4, made with the aid of a camera lucida from the margin of such a section, indicates clearly the independence of the base and the cover. Gross proof of this is also readily found in the ease with which entire covers can be removed from entire bases, leaving the margins of both structures uninjured, by rough manipulation of the cover glass in ordinary wet microscopical mounts of subcuticular species.

STRUCTURE OF THE HYSTEROTHECIAL COVER.—In the hysterothecia of certain species of Lophodermium there is present a type of construction that differs from the construction occurring in typical perithecia of the Sphaeriales or apothecia of the Phacidiales.

In *Venturia inaequalis*, investigated by Killian (1917), the perithecial wall is a development directly accompanying the process of fertilization and ascus development and is derived from the peripheral cells of the plectenchymatic knot formed by the cells of the helix. Growth of the perithecium results from the elongation and multiplication of these cells into a hollow sphere.

In *Cryptomyces Pteridis*, investigated also by Killian (1918), the origin of the apothecium is in small plectenchymatic hypostomatal knots. These give rise, from certain cells lying between the guard cells, to fertile hyphae which bore downward, as if parasitic, into the interior of the knot, while the knot itself thickens the cell walls on its outer surface and becomes a flat, brown, sclerotic mass. Eventual development of the apothecium from this point appears to occur as the result of a multiplication of the cells composing the sclerotic mass.

In *Lophodermium hysterioides*, investigated by Likhité (1926), the hysterothecia are said to arise as stromatic masses developed by a delicate secondary mycelium emanating from substomatal masses such as that shown in Plate II, Fig. 2. This has not been substantiable in my own

studies (see p. 36). But it has appeared that hysterothecia probably develop in the following manner from small knots of plectenchymatic cells as the result of radial growth of hyphae.

So far as may be determined from sectioned and macerated material, there occurs at points not specially determined an aggregation of fungous cells which become brown in color and from which emanate in a radial direction an upper and a lower plate of mycelial threads. These hyphae, in some species, tend to interweave and form a pseudoparenchyma, in others, to form a compact flat plate one cell thick. From the covering layer there is proliferated, on the underside, a mass of pseudoparenchyma which gives the cover its thickness, and in many species the basal layer is thickened by upward proliferation of cells.

It is characteristic, in all species in which the outermost layer of the cover forms a mycelial plate, that at the margin of the hysterothecium the terminations of the individual hyphae can be distinctly seen, both in the cover and in the base. In many species it is characteristic of the cover to spread out beyond the base at the margins at maturity and form a distinct fringe, or skirt; but in the course of the development of the hysterothecium the extent of the base often exceeds that of the cover. It is evident throughout that the hysterothecium is not formed as a result of haphazard proliferation of cells from a globular or disciform fundamental sclerotic mass. It is, instead, developed as the result of the radial growth of two layers of mycelial strands which emanate from a central point and terminate at the hysterothecial margin.

Examination of the fringe of hyphal ends forming the margins of hysterothecia reveals distinct kinds of mycelia. These may be divided into two groups, the first of which may be termed ordinary mycelium, and the second aliform mycelium. It is not possible to distinguish more than one type of ordinary mycelium, but there are three distinct types of aliform mycelium.

Ordinary mycelium is found in the covers and bases of hysterothecia of subepidermal species inhabiting gramineous hosts, and also in species inhabiting other hosts. In these species, although the general direction of development of the basal and covering layers is radial, the individual hyphae tend to run irregularly, interweaving and following, where epidermal cells are involved, the direction taken by the epidermal cells. The result of this growth, coupled with the cell proliferations which give thickness, is the formation of homogeneous pseudoparenchyma, usually heavily carbonized in the epidermal cells but taking a pseudocollenchymatous form elsewhere.

Aliform mycelium occurs abundantly in species that are intraepider-

mal or subcuticular. Its chief characteristic is that the individual hyphae develop in a very regular manner, usually by dichotomous branching of the apical cell, to produce either a continuous true dichotomy or a sympodium resulting from successive dichotomies. Growth is therefore truly radiate. The individual threads remain in the same plane and are closely applied to each other laterally so as to form a plate of mycelium one cell thick. In the cover the form of the cells is very regular, due, as shown in Plate I, Fig. 8, to the thickening of the hyphal walls along their lateral planes of contact; but in the base the regularity of the cells and hyphae is usually less evident. Proliferation of hyphal cells downward from the aliform layer of the cover and upward from aliform layer of the base accounts for the thickening of these two structures.

The commonest type of aliform mycelium is typically dichotomous. Cells constituting the margins of both the cover and the base show the apical indention, Plate II, Fig. 6, by which growth of this kind is accomplished. It is to this type of growth that reference is made in the description of species when the word aliform is used without modification.

Less common is the sympodial type of aliform mycelium shown in Plate I, Fig. 9. Its direction of growth is generally radial with respect to the hysterothecium but it shows more of a tendency to be influenced by the topography of the host tissues and to follow the directions taken by the host cells. Cells at the margins of hysterothecia made up of this type of mycelium are usually as typically indented as those in which complete dichotomy prevails, but neither the compact outer layer of the cover nor of the base have the aspect of complete dichotomy. The very limited growth of one of the branches of each dichotomy results in a marked turning and twisting of the paths of the branches that do grow and presents an aspect that is best described by the word meandering. The term meandering aliform mycelium, used subsequently in descriptions, refers to this condition.

The third type of aliform mycelium occurs only in *Lophodermium Thuyae*. This is very similar to the completely dichotomous aliform plate in general aspect, and its development is essentially radial. The difference lies in the fact that the branching does not occur as the result of dichotomous forking of the apical cells of the hyphal strands but as the result of a multiple branching of the apical cells. As shown in Plate II, Fig. 7, the branching apical cells swell outward on one side and a number of indentions occur along the swollen side. Between each of the indentions a branch of the hypha develops, and the young structure is much like the palm of a hand with short fingers attached. In the description of the species in which it occurs, this type of aliform structure is referred to as digitate.

THE HYSTEROTHECIAL OPENING.—As stated in the section on morphology, the slit which forms the opening of the hysterothecium has several characteristics which indicate that it is a true ostiole. In the development of the cover, the outer plate of mycelium proliferates downward along a median longitudinal line an especially heavy deposit of pseudoparenchyma. In this deposit, a narrow band running lengthwise remains uncarbonized and appears to form the dehiscence line referred to by Gäumann (1928) and termed the slit band by Darker (1932). On each side of this slit band, the pseudoparenchyma tends to become carbonized, very heavily in species such as *Lophodermium arundinaceum, L. melaleucum,* and *L. maculare.*

The slit band is not, as has been supposed, merely a line of weak tissue provided to determine the place and direction of rupture when the mechanical stresses developed at maturity become sufficient to cause breakage. It is, rather, a region in which the power of growth is for a time dormant. When the hysterothecium approaches maturity, growth is resumed in this region and results in the production, on each side of the median line, of a mass of fine, usually clavate, short filaments. Because of their location, the manner in which they are produced, and their complete spacial separation from the paraphyses (see Plate I, Fig. 5) of the hymenium, they are to be regarded as homologous with the periphyses which line the ostioles of certain sphaeriaceous fungi.

The definite construction of the labia, the fact that they are continuous with each other and form a complete border about the slit band, and the development of periphyses in the slit as it opens, indicates that the slit is morphologically an ostiole.

MYCELIUM.—Reference was made in the section on morphology to the types of mycelium present in species having different depths of host insertion. In almost all species the mycelium, whether hyaline and internal or brown and intraepidermal or subcuticular, is made up of the usual, cylindrical hyphae generally encountered in fungi of all kinds. In a few species, this cylindrical mycelium is distinguished by the fact that, beneath the cuticle and in the epidermal cells, hyphae terminate in enlarged cells which show the same lobing that is found in the terminal cells making up the margins of the hysterothecia. Figure 8, Plate II, shows this condition in *L. Miscanthi.* It is also striking that when the spot occupied by a Lophodermium colony is delimited by the development of a black stromatic border the hyphae in the stromata terminate in the same manner. *Lophodermium melaleucum, L. hysterioides,* and *L. pinastri* on Picea all possess this kind of hyphal termination. Some other species, as *L. apiculatum,* also possess relatively superficial strands of mycelium,

made up of two to many hyphae growing parallel to each other, which wander about beneath the cuticle or within the epidermal cells; and it is characteristic of these strands that they are marked at irregular intervals by the production of dichotomously indented terminal cells.

3. INTERPRETATION OF TAXONOMIC RELATIONSHIPS

TAXONOMIC interpretation of the relationships of fungi ought to be based upon the ontogeny of the fungus in question, in comparison with phylogeny exemplified by the entire class. In the case of ascomycetes, particular emphasis ought to be placed upon the processes involved in fertilization and the subsequent production of asci.

In dealing with the classification of species generally assigned to Lophodermium, this procedure is not possible. Only two attempts have been made to study the cytology of the genus (Prilleux, 1897; Likhité, 1926) and too little was learned of the details of fertilization and ascus formation to afford a basis for more than a general comparison with other types.

One is left therefore to construe taxonomic relationships by means of the characters possessed by the mycelium and fruiting structure on the basis of similarity with other groups.

On this basis, the sum of all characters shows a definite relationship with the Hemisphaeriales. The most striking suggestion of this is found in the fact that the hysterothecium is made up of a basal layer and a cover which are developed independently of each other and in the end are not united into a continuous structure. *Stigmatea Robertiani,* as shown by Klebahn (1918), develops its frutification upon a membranous layer of mycelium which lies between the cuticle and the epidermis. In this fructification there is present a basal disciform plectenchyma from which the asci and paraphyses arise. The collection of asci and paraphyses and the basal plectenchyma are inclosed beneath a hemispherical cap or lid. The outer layer of this cap is a brown and chytinized plate of aliform mycelium, very similar to the meandering type found in certain species of Lophodermium. At the periphery of the cap, the aliform plate extends beyond the edge of the basal plectenchyma and rests upon the membranous mycelial layer. It ends in an irregular and erose margin. The hyphae making up the basal membrane are themselves definitely dichotomous in their branching and radiate in waves, often forming secondary centers of radiation.

The similarity in structure between this fungus and the hysterothecia of Lophodermium is evident. The cap of Stigmatea corresponds in struc-

ture to the cover of the hysterothecium, with the exception that in the former the opening is reported to be a pore due to mechanical breaking away of tissue; and the extensive basal membrane of Stigmatea corresponds quite accurately to the much less extensive hysterothecial base of Lophodermium. In both cases it appears as though the thallus, or a portion of it, arches up and begins to thicken, while an ascigerous hymenium is formed under the arch. This pycnosis forms, in both cases, structures which can be accurately called pycnothecia.

The fact, however, that in Lophodermium the development of the basal membrane is limited to the hysterothecium, while outside it the mycelium is of the ordinary kind and is immersed in the host tissue, suggests a relationship with another of the families of Hemisphaeriales, the Polystomellaceae, although in Lophodermium the individual ascocarp is not connected with the internal mycelium by a central connecting column of hyphal threads.

A striking resemblance is found also with Lembosia, in which the thyriothecia are much elongated and provided with radially constructed covers. Lembosia, however, lacks the basal prosenchymatic layer.

The manner in which the hyphal threads are applied to each other laterally in the cover and base of Lophodermium, and the type of branching that takes place in some species (those especially that present a complete dichotomy), as well as the dichotomous indentions of the terminal cells of the individual strands, present a remarkable similarity to the method of growth and appearance of the mycelial bands constituting the thallus of many members of the Trichothyriaceae.

Against these characteristics, there stands the fact that in Lophodermium, the cover partakes of the nature of a perithecium, as shown by the development of morphological periphyses within the slit by which it opens, and thereby points a connection with certain Sphaeriales, such as Gnomonia.

SYSTEMATIC AND DESCRIPTIVE TREATMENT OF SPECIES

In this arrangement only those species of Lophodermium are being considered that have not been transferred to other genera because of the possession of criteria well recognized as of generic value. The present status of species already transferred will be found in a following section (p. 112). The species treated in this section have the following general characterization.

Parasitic or saprophytic ascomycetes with subrotund, elliptical, or linear, flattened ascocarps situated within the tissue of the host and composed of radially constructed basal and covering strata which are separate at the margins; the cover opening by an elongated ostiole surrounded by thickened or carbonized labia and lined with periphyses; the hymenium basal, arising from a closely interwoven plectenchyma of fine hyphae and consisting of both asci and paraphyses; paraphyses filamentous, simple, of uniform diameter or clavately expanded at the tips, often gelatinously united into a compact epithecium above the asci; asci cylindrical, asymmetrically rounded at the top, 4- or 8-spored; ascospores hyaline or dilutely colored, filiform, non-septate, of essentially uniform diameter throughout their length, fasciculate and arranged in pairs, frequently incased in gelatinous sheaths; mycelium internal, hyaline or brown, cylindrical, variably septate, often aliform.

KEY TO GENERA

Hysterothecia entirely pseudoparenchymatic; aliform mycelium absent
  from the cover and base:
    Hysterothecia subepidermal...............................1. Lophodermium
    Hysterothecia intraepidermal.................................2. Dermascia
Hysterothecia with a chitinized aliform plate forming the outer layer of
  the cover and the bottom layer of the base:
    Hysterothecia intraepidermal............................3. Lophodermellina
    Hysterothecia subcuticular................................4. Lophodermina

1. LOPHODERMIUM Chevallier

Flore général des environs de Paris, vol. 1, p. 435. 1826.

Lophoderma Chevallier, Journ. de Physique 94 : 31. 1822.
Aporia Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 51. 1861, in part.
Scolecodothis Miles, Mycologia 18 : 165. 1926.

Hysterothecia dull black, subrotund to linear, subepidermal in origin and insertion, often involving the epidermal cells in the cover, made up of interwoven cylindrical hyphae which are radially disposed and form independent basal and covering layers; opening a longitudinal, periphysate ostiole; hymenium basal, arising from a closely interwoven plectenchyma of fine hyphae; paraphyses filamentous, hyaline to dilutely colored, simple, indeterminate, united or not into an epithecium; asci cylindrical to subclavate, asymmetrical at the top, 8-spored; ascospores hyaline, filiform, nonseptate, of essentially uniform diameter, fasciculate and arranged in pairs, usually inclosed in a gelatinous matrix.

Type species: *Lophodermium arundinaceum* Chevallier, Flore général des environs de Paris, vol. 1, p. 435. 1826.

KEY TO THE SPECIES OF LOPHODERMIUM

Asci generally more than 125 μ long:
  Paraphyses united above the asci in an epithecium; on Pinus.....20. L. pinicolum
  Paraphyses infrequently exceeding the asci, epithecium absent or indefinite:
    Ascospores about 100 μ long; on Picea.........................7. L. crassum
    Ascospores up to 75 μ long; on Abies..........................9. L. decorum
Asci generally less than 125 μ long:
  Asci generally more than 100 μ long:
    Hysterothecia large, more than 800 μ long:
      Gelatinous ascospore sheaths conspicuous; on Pinus........10. L. durilabrum
      Sheaths not conspicuous; on Miscanthus...................18. L. Miscanthi
    Hysterothecia small, up to 800 μ long; on Convalaria.........14. L. herbarum
Asci generally less than 100 μ long:
  Paraphyses clavately enlarged above:
    Hysterothecia large 500–1000 μ long:
      Asci 80 μ or more long; on Aira.............................2. L. Airarum
      Asci not over 60 μ long; on Chamaecyparis..........6. L. Chamaecyparisii
    Hysterothecia small, seldom over 600 μ long; on Acacia......1. L. acacicolum
  Paraphyses not clavately enlarged:
    Periphyses and epithecium tinted brown or yellow:
      Asci long and thin, 85–100 × 7–8 μ; on Mangifera.......16. L. Mangiferae
      Asci broader, 70–90 × 8–10 μ; on Ampelodesmus...........11. L. eximium
    Periphyses and epithecium white:
      Hysterothecia generally more than 750 μ long:
        Hysterothecia apiculate at the ends.................3. L. Andropogonis
        Hysterothecia not apiculate:
          Labia very conspicuous, 75–100 μ wide; on Dactylis.......8. L. Dactylis
          Labia not over 75 μ wide:
            Asci slender, about 6 μ wide; on Brachypodium....5. L. Brachypodii
            Asci broader, 8–10 μ wide:
              Ascospores 1.5–2 μ wide; on various grasses...4. L. arundinaceum
              Ascospores not over 1 μ wide:
                Asci up to 100 μ long; on Secale..................21. L. Secalis
                Asci not over 70 μ long; on Sieglingia.........22. L. Sieglingiae
      Hysterothecia generally less than 750 μ long:
        Periphyses persistent...............................13. L. gramineum
        Periphyses soon evanescent:
          Labia narrow:
            Labia distinct, up to 35 μ wide; on Phleum..............19. L. Phlei
            Labia indistinct; on Rosthkovia....................12. L. fuegianum
          Labia 30–60 μ wide:
            Asci generally between 80 and 100 μ long, 9 μ wide;
              on Stipa.......................................17. L. minutum
            Asci generally less than 85 μ long:
              Ascospores 50–75 μ long; on Koeleria.............15. L. Koeleriae
              Ascospores 40–50 μ long; on Typha...............23. L. typhinum

1. *Lophodermium acacicolum* n. sp.

Hysterothecia small, dull black, amphigenous in yellow to cream colored, oval spots 1 to 3 mm. in diameter on the blades of dead leaves, few per spot, broadly oval with bluntly rounded ends and irregular, erose margins, 300–625 × 200–300 μ, subepidermal. Labia inconspicuous, car-

bonized, 30–50 μ wide, lined inwardly with greenish yellow, gelatinizing, soon evanescent, clavately expanded periphyses 1.5–2 μ wide and up to 30 μ long. Basal layer 2 to several cells thick, pseudoparenchymatous, brown, translucent, overlaid by a closely interwoven, fine plectenchyma 8–12 μ thick from which the hymenium arises. Cover well arched, entirely pseudoparenchymatic, translucent except at the carbonized margin, involving epidermal cells and in age breaking completely away. Paraphyses greenish yellow in mass, straight or flexuous, with clavately expanded tips, bent and crushed and gelatinized above the asci into a greenish yellow epithecium 15–25 μ thick, elsewhere without a gelatinous sheath, 110–130 μ long, 1–1.5 μ wide. Asci long, cylindrical, straight, bluntly and asymmetrically rounded above, tapered below into a long, fine stipe, 75–100 × 5–7 μ, 8-spored. Ascospores with a marked green tint, straight or intricately coiled near the top of the ascus, nonseptate, fasciculate and arranged in pairs, 35–75 μ long, 1–1.5 μ wide, incased in a hyaline gelatinous matrix about 1 μ thick.

Imperfect stage: Unknown.

Type locality: Wahiawa, Oahu, Hawaii.

Type specimen: Stevens, Hawaiian Fungi No. 234.

Host: *Acacia Koa:* Hawaii (Stevens, 1925).

Specimens seen: Stevens, Hawaiian Fungi No. 234, island of Oahu; No. 1156, island of Maui.

This fungus was reported by Stevens (1925) under the name *Lophodermium intermissum* Starb., but it differs from Starbach's species in important respects, aside from the fact that it is on a host belonging to the Leguminosae.

2. *Lophodermium Airarum* (Fries) Hilitzer

Hysterium culmigenum γ *Airarum* Fries, Systema Mycologicum 2 : 593. 1823.
Lophodermium Airarum Hilitzer, Vědecké spisy vydáv. Českoslov. Akad. Zeměd. 3 : 94. 1929.

Hysterothecia scattered in poorly defined, light stramineous areas on stems, leaves, and sheaths, oriented parallel with the veins, black but not shining, oblong-ellipsoid, with obtuse or rarely mucronately terminated ends, 500–1000 × 200–500 μ, subepidermal. Labia heavily carbonized, 20–35 μ wide, up to 75 μ thick, bordered inwardly by gelatinized, early deliquescent periphyses 15–20 μ long. Basal layer of 1 or 2 layers of radiately disposed, brown, translucent, non-aliform cells, this overlaid to a depth of 10–15 μ by a hyaline, columnar plectenchyma. Cover convex and well arched, black, opaque and heavily carbonized, pseudoparenchymatic, involving epidermal cells, 20–75 μ thick. Paraphyses abundant,

filiform, straight or variously bent at the apex, 1–1.5 μ wide, 80–110 μ long, enlarged at the tips and gelatinized to form a white epithecium up to 5 μ thick. Asci cylindrical to subclavate, asymmetrically subconic at the tips, somewhat attenuated toward the base and ending in a broad foot, 80–110 × 7–9 μ, 8-spored. Spores filiform, hyaline, straight or slightly twisted within the ascus, slightly attenuated at both ends, 50–80 × 1.5 μ, inclosed in a thin, hyaline, gelatinous matrix.

Imperfect stage: Belongs to the Leptostromataceae; pycnidia about 100 μ in diameter; spores not described. (Hilitzer, *l. c.*, p. 95.)

Type locality: Valley of the Kačák River, Czechoslovakia.

Type specimen: Not designated by Hilitzer.

Host: *Deschampsia flexuosa*—Czechoslovakia (Hilitzer, 1929), Germany (Jaap, 1914), Denmark (Rostrup, 1888).

Exsiccati: Sydow, Mycotheca Germanica No. 1599.

3. *Lophodermium Andropogonis* n. sp.

Hysterothecia dull black, arranged in rows between veins in extensive, light stramineous areas on sheaths and leaves, oblong with abruptly rounded ends to linear and truncate, the ends briefly apiculate in a straggling, pointed hyphal mucron of variable size, 520–1700 × 150–210 μ, subepidermal. Labia prominent, extraverted in age, heavily carbonized, 50–70 μ wide, 25–40 μ thick, involving the epidermal cells, lined inwardly with a mass of white, clavately enlarged, gelatinizing and soon evanescent periphyses 10–15 μ long by 1.5 μ wide. Basal layer a concave plate about ¾ the width of the cover and several cells (up to 15 μ) thick, consisting of carbonized and noncarbonized pseudoparenchyma, this overlaid to a depth of 12–16 μ by a very compactly interwoven and finely constructed hyaline plectenchyma from which the hymenium arises. Cover chiefly pseudocollenchymatic, translucent and not heavily carbonized except in the labia, wider than the base, involving both epidermal and hypodermal cells. Paraphyses filamentous, hyaline, straight or flexuous, simple, not expanded at the tips but interwoven above the asci into a gelatinous, white epithecium about 10 μ thick, 95–110 μ long by 1.5–2 μ wide. Asci cylindrical, straight or curved, bluntly and asymmetrically rounded at the tips, tapered from well above the middle to a long fine stipe, 80–105 μ long, 5–7.5 μ wide, 8-spored. Ascospores filiform, hyaline, nonseptate, straight or intricately coiled in the upper half of the ascus, of uniform diameter, 55–75 μ long, 0.75–1 μ wide, without evident gelatinous sheath.

Imperfect stage: Unknown.

Type locality: Peralta, Costa Rica.

Type specimen: Stevens, Fungi of Costa Rica No. 463.

Host: *Andropogon bicornis:* Costa Rica (Stevens, specimen).   ˙

4. *Lophodermium arundinaceum* (Schrader *ex* Fries) Chevallier

Plate I, Figs. 2, 7, 10; Plate II, Figs. 9, 10, 11;
Plate IV, Figs. 16, 17.

Hysterium arundinaceum Schrader, Journ. Bot. 2 : 68. 1799.
Xyloma arundinaceum Rebentisch, Prod. florae Neomarchicae, p. 342. 1804.
Hypoderma arundinaceum DeCandole, Flore française 6 : 136. 1815.
Lophoderma arundinaceum Chevallier, Journ. de Physique 94 : 31. 1822.
Hysterium arundinaceum Fries, Systema mycologicum 2 : 590. 1823.
Lophodermium arundinaceum Chevallier, Flore gén. des env. de Paris, vol. 1, p. 435.
　1826.
Lophodermium arundinaceum var. *abbreviatim* Robert & Desmazières, Ann. Sci.
　Nat. 19 : 335. 1843.
Lophodermium arundinaceum f. *vulgare* Fuckel, Symbolae mycologicae p. 256. 1869.
Lophodermium arundinaceum f. *Phragmitis* Saccardo, Michelia 1 : 410. 1878.
Lophodermium arundinaceum var. *Piptatheri* Ranojevic, Ann. Myc. 8 : 354. 1910.

Hysterothecia dull black, scattered in light stramineous or undifferentiated areas on dead leaves, sheaths, and stems, arranged in rows between veins and oriented parallel with them, broadly elliptical with rounded ends, 575–2500 × 255–1000 μ, subepidermal. Labia prominent, heavily carbonized, narrow and of generally uniform width throughout their length, often extraverted in age, frequently cracking apart at the ends of the ostiole, lined on the inner edges with a white mass of hyaline, clavately expanded, gelatinizing, more or less persistent periphyses up to 50 μ long and about 2 μ wide. Basal layer pseudoparenchymatic, several to many cells thick, brown, more or less translucent, concave, flat at the margins and there forming a shelf which supports the cover; overlaid to a depth of 10 to 50 μ by a hyaline, closely interwoven plectenchyma of fine hyphae from which the hymenium arises. Cover well arched, pseudocollenchymatic, varying from brown and translucent to well carbonized and opaque, up to 90 μ thick. Paraphyses filamentous, hyaline, straight or flexuous, not clavately expanded at the tips but variously bent or crushed and united by gelatinization above the asci into a compact white epithecium 5 to 20 μ thick, 75–130 μ long, 1.5–2 μ wide. Asci cylindrical to subclavate, acute at the asymmetrically conical tips, tapered from the middle or below to a broad or fine short or long stipe, 70–120 μ long, 7–12 μ wide, 8-spored. Ascospores hyaline, filamentous, straight or intricately coiled, nonseptate, fasciculate and arranged in pairs, of uniform diameter, 60–100 μ long, 1.5–2 μ wide, incased in a hyaline gelatinous matrix 1–2.5 μ thick.

Imperfect stage: Leptostromella hysterioides f. *graminicolum* (de Not.) Sacc., Sylloge Fungorum 3 : 659. 1884. (Rehm, 1887).

Type locality: ? Carolina (Fries, Systema Mycologicum 2 : 591. 1822).

Type specimen: Mougeot & Nestler, *Stirp. Crypt.* No. 655. The type

material on which this species should be based would be that of Schrader, whose herbarium was deposited in the herbarium of the Imperial Botanical Garden of St. Petersburg. I am informed by Dr. B. A. Keller that it is impossible to locate Schrader's original material of this species. The first exsiccatum cited by Fries, *Scleromyceti Sueciae* No. 328, was originally published as *Dothidia asteroma* and Fries was in error in citing it under *Lophodermium arundinaceum*. Next in order is Mougeot and Nestler's specimen, cited by both Fries and Chevallier, which I have examined.

Hosts: Various grasses, of which there are the following records. *Arundinaria tecta:* Carolina (Fries, 1823); *Phragmites communis:* France (Chevallier, 1826, De Thumen, *exs.*); Czechoslovakia (Hilitzer, 1929), Germany (Rehm, 1896), Bavaria (Sydow, *exs.*), Brandenberg (Sydow, *exs.*); *Ammophila* (Calamogrostis) *arundinacea:* Saxony (Kunze *exs.*); *Nardus stricta:* Italy (Ferraris, 1902); *Piptatherum paradoxum:* Serbia (Ranojevic, 1910); *Avenastrum filifolia:* Austria (Jaap, 1916); *Arundo Donax:* Austria (Jaap, 1916); *Agropyron repens:* Austria (Jaap, 1916); *Livingstonia:* Philippines (Stevens' *mss.*)

Exsiccati: Mougeot & Nestler, Stirp. Crypt. No. 655; De Thuemen, Mycoth. univ. No. 77; Sydow, Mycoth. Germ. Nos. 1172, 1598; Kunze, Fungi sel. exs. No. 160; Rabenhorst, Fungi Europ. No. 1226. See Rehm (1896) and Hilitzer (1929) for other exsiccati.

Illustrations: Schrader, Journ. Bot. 2 : pl. 3, fig. 3, 1799; Rehm, in Rabenhorst's Krypt. Flora von Deutschl. 3 : p. 31, figs. 1-5. 1896; Richon, Catal. Champ. Marne, p. 521, 1889; Lindau, Engler & Prantl, Pflanzenfamilien 1 (1) : 269, fig. 194, k-l, 1897; de Notaris, Profilo de la famiglia degli Isteriac. pl. 6, fig. 41, 1846. Brocq-Rousseu et Gain, Ennemis de l'Avoine, pl. 12, fig. 2 a-e, 1910.

Note: The material in the copy available to us of Roumeguère's Fungi Gallici exsiccati No. 166, labeled *"Hysterium (Lophodermium) arundinaceum* Schrad."* consists of two pieces of dead dicotyledonous stems, one piece apparently from a Composite the other squarish and possibly of the Labiatae. Hysterothecia typical of Lophodermina are present on both stems, subcuticular in position, distinctly aliform in cover and base, but barren of asci. The specimen is not referable to *L. arundinaceum*, but beyond that is unidentifiable.

This species, as the type of the genus, though held by Rehm (1887) to be segregated into various forms and varieties, some of which have subsequently been given specific rank, still contains a considerable heterogeneity of forms, particularly as to their host preferences. These are not easily separated from the species on constant morphological characters, or material of them has been hard to procure. It is therefore regarded

here as an inclusive species, from which further species may be segregated in the future.

5. *Lophodermium Brachypodii* Hilitzer

Plate II, Fig. 12.
Vědecké spisy vydávané Československou Akademií Zemědělskou 3 : 93. 1929.

Hysterothecia scattered in light stramineous areas of large or small extent on leaves and sheaths, narrowly elliptical to oblong with bluntly to sharply rounded ends, dull black, arranged in rows between and oriented parallel with the veins, 500–1500 × 200–500 μ, subepidermal and extending by the crushing of tissue deep into the mesophyll. Labia dark, nontranslucent, heavily carbonized, 35–80 μ wide and up to 75 μ thick, cushion like, and lined inwardly with tardily evanescent hyaline periphyses up to 20 μ long and 2 μ wide. Basal layer of brown, radiately disposed, non-aliform hyphae, 2–4 cells thick and translucent, this overlaid to a depth of 5–10 μ by a fine, hyaline, closely interwoven plectenchyma; hymenium about 90 μ thick; epithecium dull white, up to 30 μ thick, gelatinous. Cover of non-aliform and non-radiate, subcarbonized pseudocollenchymatous tissue, involving the epidermal and sometimes hypodermal cells, to 45 μ thick. Paraphyses abundant, straight or variously crushed or bent at the tips, tapered from 2 μ at the base to about 1 μ wide at the tips, up to 120 μ long, gelatinized above the asci in a white epithecium up to 30 μ thick. Asci cylindric to subclavate, tapered from near the base to a rather broad foot, obtuse and asymmetrically subconic at the tips, straight or bent by pressure, 60–90 μ long, quite uniformly 6 μ wide, 8-spored. Ascospores filiform, hyaline, subflexuous, up to 70 μ long, about 1 μ in diameter, non-septate, fascicled and arranged in pairs, without evident gelatinous matrix.

Imperfect stage: Unknown.

Type locality: Duba, Bohemia.

Type specimen: Not designated by Hilitzer.

Hosts: *Brachypodium pinnatum:* Czechoslovakia (Hilitzer, 1929), Austria (Jaap, 1916) ; *Brachypodium ramosum:* Austria (Jaap, 1916).

Exsiccati: Migula, Krypt. Germ., Aust., et Helv. exs. No. 240.

Illustrations: Hilitzer, Vědecké spisy vydáv. Českol. Akad. Zeměd. 3 : 17, fig. 6. 1929.

6. *Lophodermium Chamaecyparisii* Shirai & Hara

Botanical Magazine of Tokyo 25 : 69. 1911.

Hysterothecia scattered, black, elevated, elliptical or circular, longitudinally dehiscent, 500–800 × 300–500 μ, in cross section 300–350 μ

deep, subepidermal. Asci cylindrical or clavate, obtusely pointed at the apex, 8-spored, 50–60 × 5–5.5 μ. Paraphyses filiform, slightly swollen at the apex, simple or branched. Ascospores fascicular, filiform, 40–50 × 0.5–0.7 μ, hyaline.

Type locality: Kawauye-mura, Province of Mino, Japan.

Type specimen: Not designated.

Host: *Chamaecyparis obtusa:* Japan.

Illustrations: Bot. Mag. Tokyo 25 : *pl. 2, figs. 1, 2.* 1911.

Specimens of this species have not been seen. The description above differs somewhat from the description of the authors of the species in that it includes characteristics illustrated by the drawings, as well as those in the written description.

7. *Lophodermium crassum* Darker

Contributions from the Arnold Arboretum of Harvard University 1 : 88. 1932.

Hysterothecia scattered, amphigenous, shining black, broadly elliptical to linear, 800–2650 × 550–750 μ, subepidermal, ends rounded. Cover dark, heavily carbonized, 160–180 μ thick, consisting of pseudoparenchyma and involving epidermal cells; basal layer 1 to several cells thick, made up of a loose, light brown, large-celled plectenchyma, this overlaid to a depth of 40–60 μ by a fine, hyaline, columnar plectenchyma from which the hymenium arises; aliform structure entirely lacking. Labia heavily carbonized, thick, opening widely, and lined on the inner edges by a mass of hyaline, gelatinously agglutinated and soon evanescent periphyses up to 2 μ wide and 20–30 μ long. Paraphyses filiform, hyaline, straight, the tips not enlarged or swollen but variously bent or crushed, 120–150 μ long, 1.5–2 μ wide, incased throughout their length in a thin gelatinous matrix. Asci cylindric to subclavate, asymmetrically and somewhat bluntly rounded at the tips, tapered from below the middle into a narrow base, 140–165 μ long, 9–12 μ wide, 8-spored. Ascospores filamentous, hyaline, straight or somewhat twisted with the ascus, 90–105 μ long, 1–1.5 μ wide, fasciculate and arranged in pairs, incased in a conspicuous gelatinous matrix 1–2 μ wide.

Imperfect stage: Not named. Pycnidia subepidermal, 500–1125 × 320–490 μ, opening by a longitudinal slit along one or both lateral edges, 100–175 μ deep; basal layer of brownish colored pseudoparenchyma and hyaline plectenchyma 45–90 μ thick; conidiophores simple, 15–30 μ long; conidia bacillar, hyaline, nonseptate, 4–5 × .8–1.2 μ. (Darker, *l. c.*)

Type locality: Young's Valley, Siskiyou County, California.

Type specimen: John H. Maxson, No. 797, deposited in the Arnold Arboretum Pathological Herbarium.   .

Host: *Picea Breweriana* S. Wats.—Type locality only.

Illustrations: Darker, Contrib. Arnold Arboretum Harvard Univ. 1 : pl. 6, fig. 4. 1932.

8. *Lophodermium Dactylis* (Roumeguère) n. comb.

Plate II, Fig. 5.

Lophodermium arundinaceum f. *Dactyli* Roumeguère, in Fungi Gallici exsiccati No. 1700, 1881, and Rev. Mycol. 3 : 5. 1881.

Lophodermium Dactylidis Hilitzer, Vědecké spisy vydáv. Českosl. Akad. Zeměd. 3 : 92. 1929.

Hysterothecia black, oblong to oval, subepidermal, 750–1275 × 300– 410 μ, subepidermal, with dark brown cylindrical hyphae meandering outward subcuticularly from the ends. Labia very heavily carbonized, 75–100 μ wide, up to 60 μ thick, lined on the inner edges with a white mass of hyaline, subclavate, gelatinously agglutinated periphyses 2 μ wide by 20–35 μ long. Basal layer 1 cell thick, of radiately disposed plecten- chyma, light brown and translucent, this overlaid with a hyaline, finely composed plectenchymatic hypothecium 15–25 μ thick. Cover heavily carbonized, swollen and well rounded, composed of pseudocollenchymatic to very heavily carbonized cells involving the epidermal cells of the host, non-aliform, up to 60 μ thick. Paraphyses hyaline, filamentous, straight except at the tips which are not swollen but are often variously curved or bent and are gelatinously agglutinated into a dense white epithecium 10–30 μ thick, 85–100 × 1 μ. Asci cylindric to subclavate, 55–88 × 6–10 μ, asymmetrical and rounded to subacute at the tips, tapered below to a fine base, 8-spored. Asocospores hyaline, filiform, apparently nonsep- tate, fasciculate and arranged in pairs, 45–55 × 1–1.5 μ, gelatinous matrix inconspicuous.

Imperfect stage: Unknown.

Type locality: "Environs de Coulouse," France.

Type specimen: No. 1700 in C. Roumeguère, Fungi Gallici exsiccati.

Hosts: *Dactylis* sp.: France (Roumeguère, *exs.*); *D. glomerata:* Austria (Bubak, 1909), Czechoslovakia (Hilitzer, 1929).

9. *Lophodermium decorum* Darker

Contributions from the Arnold Arboretum of Harvard University 1 : 90. 1932.

Hysterothecia grayish-black, hypophyllous, arranged in 2 rows along the stomatal surfaces of the needles, short-elliptical, 500–1130 × 300– 560 μ, subepidermal, 250–300 μ deep when opened. Labia inconspicuous, narrow, heavily carbonized, lined inwardly by hyaline, gelatinous, soon evanescent periphyses. Basal layer of variable thickness, consisting of a

dark brown rather tightly compacted plectenchyma tending toward a pseudoparenchymatous texture, this overlaid by a hyaline, finely constructed, closely interwoven plectenchyma 10–20 μ thick, from which the hymenium arises. Cover dark, pseudoparenchymatous, rather heavily carbonized in the central portion, involving the epidermal cells, 60–100 μ thick. Paraphyses hyaline, straight, neither enlarged, swollen or bent at the tips, immersed in a thin gelatinous matrix, 130–180 μ long and about 1 μ wide, for the most part shorter than the asci and not united above them to form an epithecium. Asci cylindric to subclavate, asymmetrically rounded at the tips, gradually tapered to a narrow base, 140–185 μ long, 16–18 μ wide, 8-spored. Ascospores hyaline, continuous, fasciculate and arranged in pairs in the ascus, long-clavate, rounded at the tops and tapered to a subacute base, 55–75 μ long, 3–4 μ wide, immersed in a gelatinous matrix 4–5 μ thick.

Imperfect stage: Unknown.

Type locality: Troy, Lincoln County, Montana.

Type specimen: Herbarium of J. S. Boyce, No. 1247.

Host: *Abies grandis:* Montana (type locality) and Oregon (vicinity of Mt. Hood) (Darker, 1932).

Specimen examined: G. D. Darker, No. 2688, Zig Zag Mt. Trail, Oregon.

Illustrations: Darker, *l. c.,* pl. 26, figs. 5-7.

This appears to be a border-line species. The spore form as illustrated by Darker and as seen in an examination of his material suggests that it might readily be assigned to Hypoderma. The absence of aliform mycelium brings it into agreement with *L. arundinaceum* so far as structure is concerned; but the spores are not filiform in the same sense. Though proportionately long, their width is still great and this, with their tapered bases, their position in the ascus and their length with relation to the ascus gives a definite suggestion of the characters expected for Hypoderma.

10. *Lophodermium durilabrum* Darker

Contributions from the Arnold Arboretum of Harvard University 1 : 87. 1932.

Hysterothecia on the outer, abaxial surfaces of reddish-brown attached needles, brownish black, elliptical, well arched, 875–1750 μ long, 375–530 μ wide, subacute at the ends, subepidermal as shown by the marginal insertion, 175–230 μ deep, occurring singly or in pairs in short sections of the leaf marked off by heavy, black, stromatic lines. Labia thick, rather heavily carbonized, 50–70 μ wide, lined inwardly at maturity by gelatinous, septate, hyaline, clavate, soon evanescent periphyses. Basal layer a very loose brown plectenchyma one to several cells thick over-

laid by a finely woven, compact hyaline plectenchyma 20–30 μ thick, from which the hymenium arises. Cover 60–75 μ thick, involving the epidermal cells and, toward the center, the hypodermal cells, consisting of poorly carbonized cells pseudoparenchymatous except in the region between the lips of young hysterothecia where they are elongated and in vertical rows and develop upon the maturity of the hysterothecium into the periphyses. Paraphyses hyaline, filiform, nonseptate, straight, clavately expanded at the tips, 100–130 μ long, about 1 μ wide, encased throughout their length in a conspicuous gelatinous matrix 1.5–2 μ thick. Asci cylindric to slenderly sub-clavate, tapered abruptly to an asymmetrically acute tip, narrowed toward the base to a fine, short stalk, 100–130 μ long, 8–10 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasiculate and arranged in pairs, 90–110 μ long, 1 μ or somewhat less in width, incased in a conspicuous gelatinous matrix 1–2 μ thick.

Imperfect stage: Unknown.

Type locality: Horsethief Meadows, Hood River County, Oregon.

Type specimen: L. N. Goodding and G. D. Darker, No. 157, in Arnold Arboretum Pathological Herbarium.

Host: *Pinus monticola:* type locality only.

Illustrations: Darker, *l. c.,* pl. 26, figs. 1-3.

11. *Lophodermium eximium* de Cesati

Rabenhorst's Fungi Europaei et extraeuropaei exsiccati No. 2643a. 1881, and Hedwigia 21 : 7. 1882.

Lophodermium Ampelodesmi de Cesati, in literature.

Hysterothecia scattered in large, irregular, stramineous spots set off from unattacked tissue by a fine, black, stromatic line 50–150 μ wide, arranged between and parallel with the veins of the sheaths, usually discrete but becoming confluent end-to-end, dull to shining black, oblong-elliptic with bluntly rounded ends and symmetrically arched cover, 525–900 μ long, 250–525 μ wide, subepidermal. Labia tending to be extroverted, heavily carbonized, and lined inwardly with a prominent and conspicuous mass of white to cream-colored periphyses. Basal layer 2 to 4 cells thick, of well browned but not carbonized pseudoparenchyma, this overlaid by a layer of closely interwoven, hyaline plectenchyma 10–20 μ thick. Cover of variable thickness, composed of partially carbonized pseudocollenchyma and involving some or all of the epidermal cells; aliform mycelium entirely absent. Paraphyses abundant, straight or somewhat flexed, exceeding the asci by as much as 20 μ and united above by gelatinization into a definite brown but thin epithecium, the tips neither swollen nor curved but usually variously bent and crushed by pressure, up to 110 μ long and usually about 1 μ or less wide. Asci cylindrical,

bluntly rounded or subacutely asymmetrical at the apex, below this taper-
ing gradually to a very fine stipe, 70–90 × 8–10 μ, 8-spored. Ascospores
filiform, nonseptate, hyaline, fasciculate and arranged in pairs, straight or
somewhat twisted with the ascus, 50–70 μ long, about 1 μ thick, incased in
a hyaline gelatinous sheath 1.5–2 μ thick.

Imperfect stage: Unknown.

Type locality: "Neapolitano, in H. B. (Catanensibus)."

Type specimen: Rabenhorst, Fungi Europaei, No. 2643a.

Host: *Ampelodesmus tenax:* Italy (Rabenhorst, *exs.*)

Exsiccati: Rabenhorst, Fungi Europaei, No. 2643a.

Remarks: In Cesati's original description, the asci are said to measure
135 μ long and 10 μ wide. In our examination of the type material we
have been unable to find any asci exceeding 90 μ in length, though the
paraphyses do much exceed them and might in some material reach
the length reported for the asci.

12. *Lophodermium fuegianum* Spegazzini

Plate V, Fig. 5.

Fungi Fuegianum No. 306. 1887. In Bol. Acad. nac. de Cien. Cordoba 11 : 135-311.
1887.

Hysterothecia minute, shining black, closely crowded and often
laterally confluent in small, indefinite, unlimited, light, stramineous areas
on stems, oriented parallel to the stem axis, elliptical with abruptly or
gently rounded ends, 390–700 μ long, 200–300 μ wide, subepidermal.
Labia very indistinct, dark brown and translucent, bordered inwardly by
deliquesced masses of periphyses, cover heavily carbonized and opaque
except in the region of the labia, involving the epidermal cells, composed
of an outer, carbonized region and an inner, dark brown pseudocol-
lenchyma. Basal layer a concave plate two to several cells thick, com-
posed of dark brown pseudoparenchyma; this overlaid to a depth of
6–10 μ by a hyaline, closely interwoven plectenchyma from which the
hymenium arises. Paraphyses hyaline, filamentous, straight or flexuous,
not clavately expanded but variously bent and crushed by pressure above
and gelatinously agglutinated to form a white epithecium up to 10 μ thick,
60–85 μ long, 1–1.5 μ wide. Asci cylindrical to subclavate, asymmetrically
rounded and obtuse at the apex, abruptly tapered near the base to a short,
broad stipe, 60–80 μ long, 5–6.5 μ wide, 8-spored. Ascospores hyaline,
filiform, nonseptate, fasciculate and arranged in pairs, straight or some-
what twisted with the ascus, 40–55 μ long, 1–1.5 μ wide, without a con-
spicuous gelatinous matrix.

Type locality: Staten Island, Tierra del Fuego.

Type specimen: Herbario Spegazzini No. 1007, in Museo de La Plata.

15. *Lophodermium Koeleriae* Hilitzer

Hysterothecia scattered in light stramineous areas on dead leaves and sheaths, arranged parallel with the veins, dull black, minute, broadly elliptic, with obtusely rounded ends, subepidermal, 300–600 × 200–400 μ. Labia heavily carbonized, up to 60 μ wide, lined inwardly by white, gelatinized, filiform periphyses. Basal layer of radiately disposed, non-aliform, brown, translucent cells, usually but one cell thick, this overlaid by a finely interwoven, columnar plectenchyma up to 15 μ thick. Cover well carbonized, non-aliform, including epidermal and sometimes parenchyma cells, 25–45 μ thick, well rounded. Paraphyses abundant, straight, hyaline, the tips neither swollen nor curved but usually much bent or crushed, 75–95 × 1 μ, united above in a shining white gelatinous epithecium about 5 μ thick. Asci cylindrical to subclavate, broadly and obtusely conical and asymmetrical at the apex, tapered below to a broad stipe, 70–85 × 6–9 μ; 8-spored. Ascospores hyaline, filiform, continuous, fasciculate and arranged in pairs, 50–75 μ long, about 1 μ thick but somewhat attenuated below and above, incased in a hyaline, gelatinous matrix about 1 μ thick.

Imperfect stage: Unknown.

Type locality: Habr, Bohemia.

Type specimen: Not designated.

Host: *Koeleria cristata:* Bohemia (Hilitzer, 1929), Germany (Hilitzer, 1929).

16. *Lophodermium Magniferae* Koorders

Hysterothecia scattered in very light stramineous spots on dead leaves, the spots extensive, merged into the darker unattacked parts and without black marginal stromatic mycelial compacts, scattered, dull black on the lamina but shining black on the nerves, strictly hypophyllous, broadly oval in outline with gradually rounded ends, 830–1250 × 415–520 μ, rather flat on top but with protruded labia, subepidermal and without aliform mycelium. Labia heavily carbonized, 50–65 μ wide, up to 30 μ thick, lined inwardly by a dense mass of filiform periphyses 3 μ wide and 30–50 μ long, clavately enlarged at the tips and orange brown in mass. Basal layer 2 to several cells thick, light brown and translucent, the hyphae radiately disposed but not aliform, this overlaid by a finely interwoven, only slightly columnar, hyaline plectenchyma up to 20 μ thick. Cover distinct at the edges from the base, thin at the margins and tending to become thicker and carbonized near the lips, non-aliform in structure, involving the epidermal cells. Paraphyses filiform, hyaline, straight,

exceeding the asci by about 10 μ, about 1 μ in diameter, not expanded or curved at the tips but crushed and gelatinous, forming a heavy yellow-tinted epithecium. Asci cylindrical to subclavate, straight or bent near the base, asymmetrically and subacutely rounded at the tips, tapered from near the base to a broad stipe, 85–100 × 7–8 μ; 8-spored. Ascospores hyaline, nonseptate, filamentous, fasciculate and arranged in pairs, straight or only slightly twisted with the ascus, 75–90 μ long, 1–1.5 μ wide, uniform in diameter and blunt at each end, inclosed in a thin, hyaline, gelatinous matrix.

Imperfect stage: Unknown.

Type locality: Not given.

Type specimen: Not given.

Hosts: Mango (*Mangifera indica* L. ?): Java (Koorders, 1907), Porto Rico.

Illustrations: Koorders, Bot. Untersuch. Java Pilze p. 163, fig. 6. 1907.

Specimen seen: Seaver & Chardon, Explorations of Porto Rico, No. 1275.

17. *Lophodermium minutum* Hilitzer

Hysterothecia scattered in light stramineous areas on the leaf sheaths, oriented parallel to the veins, very dark to black, elliptical, with obtusely rounded ends, 400–700 × 200–300 μ, subepidermal, subrotund in cross section, inserted on a tenuous weft of dark mycelium. Labia heavily carbonized, up to 65 μ thick, 30–50 μ wide, lined inwardly by tardily evanescent, hyaline periphyses 10 30 μ long, hyaline and clavately enlarged at the tips. Basal layer 1 cell thick, consisting of subradiately arranged, brown, translucent hyphae, this overlaid by a finely interwoven hyaline hypothecium 20–25 μ thick; hymenium 90–110 μ thick, overlaid by a dull white, gelatinous, very thin epithecium. Cover rotund, 20–65 μ thick, involving the epidermal cells and consisting of pseudocollenchymatic to heavily carbonized cells. Paraphyses hyaline, filamentous, simple, straight or variously bent at the tips by pressure, 80–110 μ long and about 1 μ wide, gelatinized at the tips into a thin epithecium. Asci cylindrical to subclavate, asymmetrically subconical and blunt at the apex, tapered below into a broad stipe, 80–100 by quite uniformly 9 μ, 8-spored. Ascospores filiform, straight or somewhat twisted with the ascus, hyaline, fasciculate and in pairs, 60–80 × 1 μ, inclosed in a hyaline gelatinous matrix 1–1.5 – thick.

Imperfect stage: Unknown.

Type locality: Doly, Czechoslovakia.

Type specimen: Not designated.

Host: *Stipa pennata:* Czechoslovakia (Hilitzer, 1929).

18. *Lophodermium Miscanthi* n. sp.

Plate II, Fig. 8; Plate III, Fig. 1.

Hysterothecia dull black, in extensive and indefinite stramineous spots on leaves and sheaths, broadly elliptical to linear, 650 μ to 3 mm. long, 450–650 μ wide, subepidermal. Labia heavily carbonized, narrow and of uniform width, 20–35 μ wide, up to 30 μ thick, lined on the inner edges with a white mass of hyaline, filamentous, gelatinizing and soon evanescent periphyses 10–15 μ long and 1–1.5 μ wide. Basal layer a brown, translucent pseudoparenchyma 2 or more cells thick, this overlaid to a depth of 20–30 μ by a hyaline, closely interwoven plectenchyma of very fine hyphae, from which the hymenium arises. Cover well arched, carbonized at the margins and in the labia, elsewhere brown and more or less translucent, pseudoparenchymatic, involving the epidermal cells in and near the labia, individual strands aliform, running within the lumina of the cells and ending in enlarged, dichotomoid cells. Paraphyses straight or flexuius, filamentous, hyaline, nonseptate, not expanded apically, bent or crushed at the tips and united by gelatinous matrices into a white epithecium 10–20μ thick, 90–150 μ long, 1 μ or less wide. Asci cylindrical to subclavate, asymetrically and bluntly rounded above, tapered near the base to a broad stipe and foot, 95–120 μ long, 6–8 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, straight or twisted with the ascus, fasciculate and arranged in pairs, 70–100 μ long, 0.75–1 μ wide.

Imperfect stage: Unknown.

Type locality: Mt. Maquiling, near Los Baños, Province of Laguna, Philippines.

Type specimen: Baker, Fungi Malayana, No. 155.

Host: *Miscanthus sinensis:* Philippines (Baker, *exs.*; Sydow, 1913, Stevens' mss.).

Exsiccati: Baker, Fungi Malayana, No. 155.

The great length of the hysterothecia, as well as the length of asci and spores separate this from *L. arundinaceum.* The mycelium in cells at the edge and in the cover of the hysterothecia appears to be of an aliform nature, but the occurrence of this type of mycelium is usually limited to the edge of the hysterothecium around which it forms a sort of skirt. It does not extend, as a superficial plate, over all the top of the hysterothecium.

19. *Lophodermium Phlei* n. sp.

Plate III, Fig. 2.

Hysterothecia scattered in light stramineous spots of variable size and extent on sheaths and leaves, shining black, oriented parallel with the veins 450–900 μ long by 225–450 μ wide, oblong, elliptical with nearly

straight sides and bluntly rounded ends, slit eventually splitting the entire length of the cover, subepidermal. Labia heavily carbonized, 25–35 μ wide and up to 60 μ thick, spreading widely and becoming extraverted with age, about ⅔ the length of the hysterothecium and lined inwardly by a mass of white, shining, gelatinous, soon evanescent periphyses up to 3 μ wide, 15–30 μ long, and clavately enlarged at the ends. Basal layer 1 to 2 cells thick, consisting of brown, translucent, radiately disposed plectenchyma, this overlaid by a layer of finely interwoven, hyaline plectenchyma 15–20 μ thick. Cover heavily carbonized only at the margins, involving epidermal cells and merging rather indefinitely into a loose weft of brown cylindrical, meandering mycelium within and below the epidermal cells. Paraphyses filamentous, straight or flexuous, not swollen or curved but variously bent by crushing at the apex and there interwoven into a loose, nongelatinous epithecium, up to 100 μ long and 1 μ or less wide. Asci long cylindrical to subclavate, asymmetrically subacute at the apex, somewhat tapered to a broad base or to a long stipe, 60–70 × 5–9 μ, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, 50–60 by about 1 μ, incased in a thin, hyaline gelatinous matrix.

Imperfect form: Unknown.

Type locality: Newfield, New Jersey.

Type specimen: Ellis, North American Fungi No. 465.

Host: *Phleum pratense:* type locality only.

Exsiccati: Ellis, N. Amer. Fungi No. 465.

20. *Lophodermium pinicolum* n. nom.

Plate IV, Fig. 12.

Hysterium pinastri Schrader, Schrad. Jour. Bot. 2 : 69. 1799, in part.
Hysterium limitatum Wiebel, Primitiae Florae Werth. p. 329. 1799, in part.
Hypoderma pinastri De Candolle, in Lamarck and De Candolle, Flore Français, 3rd Ed. 2 : 305. 1815.
Hysterium pinastri Fries, Systema Mycologicum vol. 2 : p. 587. 1823, in part.
Hypodermium sparsum Link, Sp. Plant. 6 (2) : 88. 1824, in part.
Aporia obscura Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 63. 1861, in part.
Depazea linearis Rostrup, Tidsskr. Skovbr. 6 : 260. 1883, in part.
Schizothyrium obscurum Saccardo, Sylloge Fungorum 2 : 725. 1883, in part.
Lophodermium baculiferum Mayr, Die Waldungen von Nordamerica, p. 313. 1890.
Scolecodothis pinicola Miles, Mycologia 18 : 165. 1926. (In part ?).
Lophodermium australe Dearness, Mycologia 18 : 242. 1926.
Lophodermium Laricis Dearness, Mycologia 18 : 243. 1926.
Lophodermium pinastri (Schrader *ex* Fries) Cheval., *pro* Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : 69. 1932.

Hysterothecia dull to shining black, amphigenous, one to several in longitudinal sections of the leaf on most hosts sharply marked off by heavy, black stromatic lines from adjacent sections, the leaf breaking

readily along these lines, elliptical with subacute ends, 700–1750 μ long by 300–750 μ wide, subepidermal, 150–350 μ deep. Labia prominent, very long, heavily carbonized, up to 90 μ wide, tapered somewhat toward each end, opening widely, lined inwardly by a layer of hyaline, papillate, gelatinous, soon evanescent periphyses. Basal layer of colorless or slightly brown translucent pseudoparenchyma, this overlaid by a fine, hyaline, closely interwoven plectenchyma 15–30 μ thick from which the hymenium arises. Cover a brown plectenchyma, chiefly pseudocollenchymatic, thin at the edges, 30–45 μ thick, heavily carbonized in the lip region. Paraphyses filiform, hyaline, simple, nonseptate, clavately enlarged at the tips, 100–165 μ long, 1.5–2 μ wide, forming a gelatinous, white epithecium 10–15 μ thick. Asci cylindrical to subclavate, asymmetrically subacute at the apex, tapered from about the middle to a short, fine stipe, 120–150 μ long, 10–14 μ wide, 8-spored. Ascospores filiform, hyaline, nonseptate, bluntly rounded at both ends, lying straight in the ascus or tending to become intricately coiled in the upper half, 85–140 μ long, 1.5–2 μ wide, incased in a hyaline, gelatinous matrix about 2 μ thick.

Imperfect stage: Leptrostroma pinastri Desm., Ann. Sci. Nat. 19 : 338. 1843, according to Diedicke (1913). *Gloeosporium Pini* Oudeman, Nederl. Kruidkund. Arch. ser. 3, 2 : 754. 1902, according to v. Luyk (1923).—Pycnidia subepidermal, elliptical, 300–500 × 85–100 μ; conidia bacillar, 6–9.5 × less than 1 μ (about .5).

Type locality: Not given by Schrader or Fries.

Type specimen: Not in existence, Fries cites *Scl. Succ. exs.* No. 50.

Hosts: *Pinus*, sp. undet.: Japan (Darker, 1932), Italy (Traverso, 1903) ; *P. albicaulis*: Oregon (Darker, 1932) ; *P. Armandi*: Massachusetts (Darker, 1932) ; *P. attenuata*: Oregon (Darker, 1932) ; *P. Banksiana*: Michigan, Minnesota, Wisconsin (Davis, 1914), Ontario, Manitoba (Bisby, 1924), Quebec (Darker, 1932): *P. contorta*: California (Boyce, spec.), Oregon, Wyoming, British Columbia (Darker, 1932), Denmark (Rostrup, 1888) ; var. *latifolia*: Colorado (Clements, *exs.*), Montana (Rhoads, spec.), Alberta (Darker, 1932) ; *P. echinata*: Arkansas (Darker, 1932) ; *P. excelsa*: India (Darker, 1932) ; *P. Jeffreyi*: California (Darker, 1932; Boyce, spec.), Washington (Darker, 1932; Boyce, spec.) ; *P. koraiensis*: Massachusetts, Jugoslavia (Darker, 1932) ; *P. monticola*: Massachusetts (Darker, 1932) ; *P. mugo*: Massachusetts (Darker, 1932) Illinois, Austria (Jaap, 1908), Denmark (Darker, 1932), Germany (Jaap, 1905) ; var. *rotundata*: Germany (Tubeuf, 1901, 1910) ; *P. nigra*: Denmark; var. *austriaca*: Oregon, Ontario (Darker, 1932), Italy; var. *cebennensis*: Denmark (Darker, 1932) ; *P. occidentalis*: Santo Domingo (Toro, 1927) ; *P. parviflora*: California, Massachusetts (Darker, 1932) ; *P. Pinaster*: Denmark (Darker, 1932) ; *P. ponderosa*: Cali-

fornia (Meinecke, spec.), Idaho, Massachusetts, Montana, Oregon, Pennsylvania, Washington, Wyoming (Darker, 1932); *P. radiata*: California (Boyce, spec.), New Zealand (Anon., 1919); *P. resinosa*: Maine, Massachusetts, New Hampshire, Ontario, Quebec (Darker, 1932); *P. rigida*: Maine, Massachusetts, New Jersey, Pennsylvania (Darker, 1932; Orton, spec.; Orton and Hass, spec.; Overholts, spec.), Denmark, Germany; *P. sabiniana*: California (Darker, 1932; Boyce, spec.); *P. sylvestris*: Massachusetts, Quebec (Darker, 1932), Austria (Keissler, 1907), Bulgaria (Malkoff, 1908), Carinthia, Denmark, Germany (Jaap, 1905), Norway (Darker, 1932), Russia (Darker, 1932), Scotland (Darker, 1932), Sweden (Darker, 1932); *P. cembra*: Austria (Jaap, 1908); *P. halepensis*: Austria (Jaap, 1916); *P. Strobus*: Maine, Massachusetts, Ontario (Darker, 1932), Wisconsin (Davis, 1914), Germany; *P. Taeda*: Florida, Louisiana (Darker, 1932), Mississippi (Miles, 1926), North Carolina (Darker, 1932).

Exsiccati: Cooke, Fungi Brit. exs. No. 396; Krieger, Fungi Saxonici Nos. 383, 1170, 1171; Petrak, Mycoth. Carpat., No. 20; Rabenhorst, Fungi europaei Nos. 371, 1443, 1922; Ravenel, Fungi caroliniani, No. 40; Roumeguère, Fungi sel. exs. No. 6941; Saccardo, Mycoth. italica No. 506; Sydow, Mycoth. Germ. No. 1931; Sydow, Myc. Marsh. No. 1376; Zopf & Sydow, Mycoth. Marsh. No. 93; de Thuemen, Fungi Austriaci No. 5056; Ravenel, Fungi amer. exs. No. 322; de Thuemen Mycoth. univ. No. 282, Ellis, North American Fungi No. 675; Ravenel, Fungi amer. exs. No. 180: Clements, Crypt. Format. Colo. No. 466; Krieger, Schad. Pilze, Konigstein, without a number.

Specimens: E. P. Meinecke, Modoc Nat. Forest, July 3, 1913; Boyce, Cisco, Cal., March 16, March 22, 1919; Wind River Nursery, Wash., May 17, 1916; C. R. Orton, Pine Grove Mills, Pa., Aug. 30, 1913; C. R. Orton and A. R. Hass, Pine Grove Mills, Pa., May, 1914; A. S. Rhoads, Fishtrap, Mont., Aug. 15, 1914; L. O. Overholts, Charter Oak, Huntingdon Co., Pa., May 29, 1921.

Illustrations: Tubeuf, Arb. Biol. Abth. Rost.-u. Landw. Kaiserl. Gesundh. 2 (1) : pl. 1, figs. 1–11; pl. 2, figs. 1–24; pl. 4, figs. 1–13; pls. 5–7. 1901.—Greville, Scot Crypt. Fl. 1: pl. 60, figs. 1–4, 1823.—Schrader, Schrad. Jour. Bot. 2 : pl. 3, fig. 4. 1799.—Rostrup, Tidsskr. Skovbr. 6 : p. 259, fig. 6; p. 260, fig. 7; p. 261, figs. 8–9. 1883. *ibid.* 12 : p. 203, fig. 4a. 1891—Hagem, Zeitschr. Forst.-u. Jagdwesen 43 : Pl. 4, figs. 1–8. 1911.—Darker, Contrib. Arnold Arboretum Harvard Univ. 1 : pl. 17, figs. 11–14; pl. 18, figs. 1–9; pl. 19, figs. 1–7; pl. 20, figs. 1–3. 1932.— Hilitzer, Vědecké spisy vydáv. Českosl. Akad. Zeměd. 3 : fig. 11. 1929.— See also Saccardo, Sylloge Fungorum 19 : 1140–1141. 1910.

soon evanescent periphyses 7–12 μ long and 1–1.5 μ wide. Basal layer a plate several cells thick of brown, translucent pseudoparenchyma, the bottom layer of which is radiately disposed; this overlaid to a depth of 10–16 μ by a closely interwoven, hyaline, more or less columnar plectenchyma of fine hyphae from which the hymenium arises. Cover carbonized at the margins and in the vicinity of the labia in young hysterothecia, in old hysterothecia heavily carbonized and opaque throughout, involving the epidermal cells, consisting of several layers of pseudocollenchymatous cells. Paraphyses hyaline, filiform, straight or flexuous, not clavately expanded above but bent by pressure and, near the sides of the hymenium, tending to become markedly uncinate, gelatinously fused above the asci into a white epithecium about 10 μ thick, 65–85 μ long, 1–1.5 μ wide. Asci cylindrical to subclavate, asymmetrically acute or subacute at the tips, narrowed near the base to a short, broad stipe, 55–70 μ long, 6.5–9 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, straight or coiled in the ascus, 40–50 μ long, 0.75–1 μ wide, each incased in a conspicuous, hyaline gelatinous matrix 1–1.5 μ thick.

Imperfect stage: Unknown.

Type locality: Not given by Fries.

Type specimen: None cited by Fries.

Hosts: *Typha angustifolia:* England (Massee, 1895), Germany (Rehm, 1887); *T. latifolia:* New York (Ellis and Everhart, 1892; Peck, spec.).

Specimen examined: Charles H. Peck, without number, at Guilderland, New York, May, 18- ?, on *Typha latifolia.*

2. DERMASCIA, new genus

Hysterothecium elliptical to linear, situated intraepidermally, flattened or applanate, opening by an elongate ostiole lined with periphyses and surrounded by thick or carbonized labia; base and cover not connected at the margins. Hymenium basal and disciform, arising from a basal plectenchyma, consisting of both asci and paraphyses. Paraphyses simple, filamentous, or clavately expanded above, often forming a gelatinous epithecium. Asci essentially cylindrical. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs. Without aliform mycelium.

Genus of the Hypodermataceae, differing from Lophodermium Chevallier in being intraepidermal and from Lophodermellina von Höhnel in lacking aliform mycelium.

Type species: *Dermascia alpina* (Rehm).

KEY TO THE SPECIES OF DERMASCIA

Asci generally more than 125 μ long:
  Ascospores generally over 125 μ long; on Picea..................6. D. filiformis
  Ascospores generally less than 120 μ long; on Abies.............3. D. consociata
Asci generally less than 125 μ long
  Asci generally more than 100 μ long:
    Ascospores 1.5–2 μ wide; on Abies...............................8. D. lacera
    Ascospores generally less than 1.5 μ wide:
      Ascospores 1–1.5 μ wide; on Dracaena.....................4. D. Dracaenae
      Ascospores 0.75–1 μ wide; on Rubus........................14. D. rubiicola
  Asci generally less than 100 μ long:
    Ascospores 5 μ or more wide................................11. D. oxyasca
    Ascospores less than 3 μ wide:
      Ascospores 2–2.5 μ wide:
        Asci 12–15 μ wide; on Gramineae..........................9. D. latispora
        Asci 10–12 μ wide; on Festuca............................5. D. Festucae
      Ascospores narrower, not over 2 μ wide:
        Asci 8–12 mu wide; on Gramineae...........................1. D. alpina
        Asci 4–8 μ wide:
          Hysterothecia generally subrotund:
            Epithecium indefinite or absent; on Dilleniaceae.......13. D. rotundata
            Epithecium present; host unrecognized...............10. D. leptothecia
          Hysterothecia generally at least twice as long as wide:
            Periphyses and epithecium bright yellow; on Carex......2. D. caricina
            Periphyses and epithecium white:
              Periphyses persistent, shining white; host unknown..12. D. Reyesiana
              Periphyses evanescent; on Heteromelis............7. D. Heteromelis

1. *Dermascia alpina* (Rehm) n. comb.

Lophodermium arundinaceum var. *alpinum* Rehm, Bericht. Natur. hist. Ver. Augsburg 26 : 80. 1881.
Lophodermium alpinum Rehm, Ber. Bayer. Bot. Ges. 13 : 119. 1912.

Hysterothecia minute, dull black, arranged in rows between veins on sheaths and leaves, elliptical to broadly ovate, with rounded or indefinitely apiculate ends from which brown cylindrical hyphae straggle out in the cavities of the epidermal cells, 415–625 μ long, 185–210 μ wide, intraepidermal but entirely lacking in aliform structure. Labia prominent, heavily carbonized and opaque, 30–40 μ wide, 25–35 μ thick, arched and spreading in the middle, lined inwardly by hyaline, soon evanescent periphyses 1.5–2 μ wide, somewhat clavately expanded at the tips and 15–25 μ long. Basal layer a brown, translucent, non-aliform plate 1 cell thick, irregularly margined and distinct and unconnected with the cover; this overlaid to a depth of 5–15 μ by a very finely interwoven, hyaline, non-columnar plectenchyma which forms the hypothecium. Cover very poorly organized, except for the margin and labia, the intervening space consisting of loosely and openly interwoven strands of cylindrical brown hyphae following the direction of the host epidermal cells, without carbonization

except in the labia and in the somewhat compacted marginal region. Paraphyses filamentous, hyaline, straight or flexuous, with slightly expanded tips which are, except beneath the ostiole, greatly crushed and bent, not united by gelatinization above into an epithecium, about 1–1.5 μ wide, 70–100 μ long. Asci cylindrical to subclavate, asymmetrically acute to subacute at the tips, abruptly tapered near the base to a broad stipe, 65–95 $\times$ 8–12 μ, 8-spored. Ascospores filiform, hyaline, non-septate, sometimes straight but mostly intricately coiled within the ascus, fasciculate and arranged in pairs, rounded at the tips and tapering to a somewhat finer base, 57–85 $\times$ 1.5–2 μ, inclosed in a thin hyaline gelatinous sheath up to 1 μ thick.

Imperfect stage: Unknown.

Type locality: Not given by Rehm.

Type specimen: Rehm, Ascomyceten No. 319.

Hosts: Grasses, especially species of Sesleria and Nardus: In the high Alps (Rehm, 1887); *Elymus ambiguus:* Larkspur Dell, Colorado (Clements *exs.*)

Exsiccati: Rehm, Ascomyceten No. 319; Clements, Cryptogamae Formationum Coloradensium No. 47.

Notes: Rehm described the asci of this species as being 45–70 $\times$ 9-15 and the spores as 36–50 $\times$ 2.5-3.5 μ. In neither the exsiccatum cited by Rehm nor in the Clements specimen do we find Rehm's dimensions.

2. *Dermascia caricina* (Robert) n. comb.

Text-Fig. 1, p. 118.

Hysterium caricinum Robert, in herb., according to Desmazières, Ann. Sci. Nat., 3 ser., 8 : 180. 1847.
Lophodermium caricinum Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 59. 1861.
Aporia neglecta Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 63. 1861.
Lophodermium arundinaceum var. *caricinum* Rehm, Rabenhorst's Kryptogamen Flora 3 : 47. 1887.
Lophodermium caricinum Rehm, Rabenhorst's Kryptogamen Flora, 2nd Ed., vol. 3, p. 1248. 1896.
Lophodermellina caricina von Höhnel, Ann. Mycol. 15 : 312. 1917.

Hysterothecia dull to shining black, amphigenous, widely separated and arranged in rows between veins in extensive, stramineous spots on leaves, elliptical with rounded ends, 650–1200 μ long, 200–500 μ wide, intraepidermal. Labia carbonized, broad, indefinite, nearly as long as the hysterothecium, extraverted in age, 65–100 μ wide, up to 75 μ thick, lined inwardly by a bright yellow mass of nonseptate, clavately expanded, gelatinously agglutinated periphyses 8–15 μ long by 1–1.5 μ wide. Basal layer a light to dark brown plate one to three cells thick, consisting of

subradiately arranged prosenchymatic cells without aliform character; this overlaid to a depth of 5–20 μ by a closely interwoven, hyaline plectenchyma of very fine hyphae, from which the hymenium arises. Cover well arched, carbonized throughout, non-aliform, its margins even at the sides and erose at the ends, composed of an outer plate of closely interwoven, cylindrical hyphae and, beneath this, a layer of pseudo-collenchymatous to completely carbonize cells ranging from 5 μ thick near the margins to 75 μ thick in the region of the labia. Paraphyses filamentous, straight or flexuous, hyaline, nonseptate, simple, somewhat expanded near the tips and also much crushed and bent by pressure, 50–80 μ long, 0.75–1 μ wide, gelatinously aggulutinated above the asci and forming a pale to bright yellow epithecium about 10 μ thick. Asci cylindrical to long-subclavate, asymmetrically and acutely conical above, tapered from above the middle to a long, thin stipe, 45–70 μ long, 4–6.5 μ wide. Ascospores hyaline, nonseptate, filiform, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, of uniform diameter, 35–60 μ long, 0.75–1 μ wide, gelatinous sheath inconspicuous.

Imperfect stage: Leptostroma caricinum Fries (Observ. mycol. praecip. ad illustr. floram Suec., p. 361. 1824) according to Fuckel (see Rehm, 1887). Karsten (Acta Soc. pro Fauna et Flora Fenn. 6 : 77. 1890) and Schroeter (Jahresber. Schles. Ges. f. vaterl. Cult. 47 : 179. 1870) have described a pycnidial stage with hyaline conidia 4–5 μ long and 0.5–1 μ wide. In the exsiccatum available to us there is an associated imperfect form classifiable as a *Gloeosporium*, with acervuli nearly concolorous with the host, 90–150 μ in diameter and producing subpyriform conidia 2–2.5 $\times$ 4.5–6 μ.

Type locality: Not given by Desmazières.

Type specimen: Desmazières, Plantes Crypt. du Nord de la France, ser. 2, No. 168. (See Duby, 1861).

Hosts: Carex spp: New Jersey (Ellis and Everhart, 1892); *C. acuta* (Rehm, 1887); *C. glauca* (Rehm, 1887, Roumeguère, exs.); *C. panicea* (Rehm, 1887), *C. paniculata:* France (Rehm, 1886).

Exsiccati: Roumeguère, Fungi sel. exs. No. 7142. Rehm cites: Fuckel, Fungi rhen. No. 1751 and Rabenhorst, Herb. myc. II, No. 723.

3. *Dermascia consociata* (Darker) n. comb.

Lophodermium consociatum Darker, Contrib. Arnold Arboretum Harvard Univ. 1 : 79. 1932.

Hysterothecia grayish black, mainly hypophyllous on needles first attacked by *Hypoderma robustum*, subcircular to broadly elliptical, 400–650 $\times$ 525–1700 μ, intraepidermal. Labia carbonized, 50–70 μ wide,

up to 130 μ thick, lined inwardly by a white mass of hyaline, clavately expanded gelatinously agglutinated and soon evanescent periphyses 1–1.5 μ wide and 15–30 μ long. Basal layer a brown, translucent, pseudoparenchymatic plate 1 to several cells thick, 16–20 μ thick; this overlaid to a depth of 10–15 μ by a closely interwoven, hyaline plectenchyma from which the hymenium arises. Cover a dark brown, more or less translucent pseudoparenchyma carbonized at the margins and in the labia, 75–130 μ thick. Paraphyses hyaline, filamentous, straight or flexuous, somewhat enlarged at the tips and the longest variously bent and crushed, mostly shorter than the asci and forming no epithecium, 150–180 μ long, about 1 μ wide. Asci cylindrical to narrowly subclavate, 150–180 μ long, 15–18 μ wide, asymmetrically subacute at the tips, tapered from about the middle to a broad base, 8-spored. Ascospores hyaline, filiform, fasciculate and arranged in pairs, nonseptate, abruptly rounded at the apices and tapered to somewhat finer bases, 95–120 μ long, 2–2.5 μ wide, incased in a hyaline gelatinous sheath 2–3 μ thick.

Imperfect stage: Unknown.

Type locality: Government Camp, Oregon.

Type specimen: Darker, July 1929, Government Camp, Oregon (Arnold Aboretum Pathological Herbarium No. 268).

Host: *Abies amabilis:* District south of Mt. Hood, Oregon (Darker, 1932); Washington (Boyce, spec.).

Specimen: J. S. Boyce, Silverton, Wash., May 22, 1916.

Illustrations: Darker, *l. c.,* pl. 21, fig. 10.

4. *Dermascia Dracaenae* (Phil. & Harkn.) n. comb.

Lophodermium Dracaenae Phillips and Harkness, Grevillea 12 : 84. 1884.

Hysterothecia dull or shining black, amphigenous and scattered in light stramineous, unlimited, small to very large spots on leaves, broadly elliptical to oblong, 330–1600 μ long, 225–525 μ wide, sometimes confluent end-to-end, intraepidermal. Labia heavily carbonized, straight and uniform in width, nearly as long as the hysterothecia, tending to become extroverted and cracking with age, 65–110 μ wide, 12–30 μ thick, lined inwardly by a brown-tinted mass of filamentous, clavately expanded, gelatinizing and very soon evanescent periphyses 8–20 μ long and 1–1.5 μ wide. Basal layer a dark brown, hardly translucent plate several cells thick, consisting of compact pseudoparenchyma without evident radial disposition; this overlaid to a depth of 8–15 μ by a closely interwoven, orange-tinted plectenchyma of fine hyphae from which the hymenium arises. Cover much arched, carbonized throughout, non-translucent except at the erose margins, composed of an outer, carbonized plate un-

derlaid, in the region of the labia to depth of 30 μ by brown pseudo-collenchyma, non-aliform at the margins. Paraphyses hyaline, filiform, non-septate, simple, straight or flexuous, not clavately expanded but variously crushed or bent at the tips and gelatinously united above the asci in a brown epithecium 15–20 μ thick, 120–150 μ long, 1–1.5 μ long. Asci long cylindrical, abruptly and asymmetrically rounded above, tapered from above the middle to a long, fine stipe, 90–130 μ long, 5–6.5 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, straight or intricately coiled within the ascus, 60–85 μ long, 1–1.5 μ long, incased in an inconspicuous, hyaline gelatinous matrix.

Imperfect stage: Unknown.

Type locality: San Francisco, California.

Type specimen: Harkness, No. 2514, May, 1881 (in herb. California Academy of Science).

Host: *Dracaena* (*fragrans?*): California (Harkness, specimen; Phillips and Harkness, 1884; Ellis and Everhart, 1892).

Note: The branched paraphyses described by Phillips and Harkness may be attributed to the fact that the hymenia in some hysterothecia are parasitized and the conidiophores of the Penicillium that is present stand among the paraphysis tips. The spore and ascus measurements given above greatly exceed those of the original description as well as those given by Ellis and Everhart (1892), but are nevertheless taken directly from the type specimen.

5. *Dermascia Festucae* (Roumeguère) n. comb.

Plate I, Fig. 1: Plate III, Figs. 3, 4.

Lophodermium culmigenum f. *Festucae* Roumeguère, Fungi Selecti Exsiccati No. 7143, 1897, and Rev. Mycol. 19 : 55. 1897.

Hysterothecia brownish black, epiphyllous, scattered and well separated, situated between veins and oriented parallel with them, not associated with discolored spots, not heavily carbonized, elliptical with truncately rounded ends, 150–180 × 375–600 μ, intraepidermal. Labia well defined, carbonized, 17–22 μ wide, about three-fifths as long as the hysterothecium, opening only narrowly to expose but a small part of the hymenium, lined inwardly with a white mass of gelatinous, soon evanescent, clavately expanded hyaline periphyses 8–15 μ long by 1.5–2 μ wide. Basal layer a very thin, brown tinted plectenchyma; this overlaid by a very closely interwoven layer of hyaline plectenchyma up to 5 μ thick from which the hymenium arises. Cover very thin, consisting of a loose weft of brown, cylindrical, somewhat branched hyphae following the cavities of the epidermal cells. External mycelium hyaline, remotely

septate, 4–4.5 μ wide.   Paraphyses filamentous, hyaline, simple, of uniform diameter, crushed or bent above the asci and gelatinized into a thick white epithecium, 90–110 μ long, 1.5–2 μ wide.   Asci cylindrical to subclavate, asymmetrically rounded to subacute at the tips, tapered somewhat from near the base to a broad, short stipe, 75–100 μ long, 10–12 μ wide, 8-spored.   Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, 65–90 μ long, 2–2.5 μ wide, usually tortuously twisted or intricately coiled in the upper half of the ascus, gelatinous matrix inconspicuous.

Imperfect stage: Unknown.

Type locality: Not known.

Type specimen: Roumeguère, Fungi Selecti Exsiccati No. 7143.

Hosts: *Festuca rubra:* France (?) (Roumeguère, exs.) ; var. *arenaria:* Bernard Harbor, Canada (Dearness, 1923) ; *F. ovina:* Switzerland (Jaap, 1907).

6. *Dermascia filiformis* (Darker) n. comb.

Lophodermium filiforme Darker, Contrib. Arnold Arboretum Harvard Univ. 1 : 85. 1932.

Hysterothecia shining black, chiefly hypophyllous, linear with acute ends, from about 900 μ to nearly as long as the leaf, 250–260 μ wide, 250–300 μ deep, occurring singly and, if more than one infection is present, these separated by a distinct, double, black stromatic line along which the leaf readily breaks.   Labia heavily carbonized, up to 80 μ wide but not very distinct, 50 to 65 μ thick, lined inwardly by a mass of hyaline or subhyaline, very short periphyses up to 8 μ long by 1.5–2 μ wide, these usually persistent and not gelatinized.   Basal layer a loose, brown to subhyaline, translucent plectenchyma 1–2 cells thick; this overlaid to a depth of 20–25 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises.   Cover consisting of a dark, usually heavily carbonized pseudoparenchyma 50–65 μ thick.   Paraphyses filiform, hyaline, straight or flexuous, slightly enlarged at the tips and gelatinously united above the asci into a white epithecium 10–20 μ thick, 140–180 μ long, 1–1.5 μ wide.   Asci cylindric, abruptly and asymmetrically subacute at the tips, narrowed below to a long thin stipe, 130–160 μ long, 15–18 μ wide, 8- or sometimes only 4-spored.   Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, 115–160 μ long, 2.5–3 μ wide, each incased in a conspicuous, hyaline, gelatinous matrix about 3 μ thick.

Imperfect stage: Not named. Darker (1932) describes an associated conidial form as follows: "Pycnidia minute, applanate, waxy, inconspicuous, more or less concolorous with leaf surface. Conidia bacillar to

allantoid, 5–9.5 × 0.8–1.2 μ." This stage was not observed in the portion of the type specimen seen by the writer.

Type locality: Bear Island, Lake Timagami, Ontario, Canada.

Type specimen: G. D. Darker No. 1695, July 1, 1926 (Arnold Arboretum Pathological Herbarium No. 822).

Hosts: *Picea glauca:* Ontario, Quebec; *P. Engelmanii:* Colorado; *P. mariana:* Ontario (Darker, 1932).

Illustrations: Darker, Contrib. Arnold Arboretum Harvard Univ. 1 : pl. 25, figs. 5–10. 1932.

7. *Dermascia Heteromelis* (Phillips & Harkness) n. comb.

Hypoderma Heteromelis Phillips and Harkness, Grevillea 13 : 23. 1884.
Lophodermium Heteromelis Ellis and Everhart, North American Pyrenomycetes, p. 718. 1892.

Hysterothecia dull black, epiphyllous or hypophyllous, scattered but numerous in light, stramineous, indefinite spots up to 1 cm. in diameter, broadly oval with rounded ends, the more elongated ones lunate, sometimes also confluent, 500–675 μ long, 300–375 μ wide, intraepidermal. Labia carbonized, indistinct, ¾ the length of the hysterothecia, not arched and not extroverted, erose on the inner margins, 20–45 μ wide, lined inwardly by a white mass of hyaline, clavately enlarged, gelatinous and very soon evanescent periphyses 8–14 μ long by 1.5–2 μ wide. Cover somewhat arched, heavily carbonized except for triangular areas at the ends, margins erose and conforming to the outlines of the epidermal cells occupied. Basal layer a light brown, translucent plate, 2 to several cells thick, composed of non-aliform, radiately disposed prosenchyma; this overlaid to a depth of 8–12 μ by a closely interwoven hyaline plectenchyma of fine hyphae from which the hymenium arises. Paraphyses hyaline, filamentous, straight or flexuous, not clavately expanded but variously crushed and bent at the tips, exceeding the asci in height and forming an epithecium 8 to 15 μ thick above them, 90–135 μ long, 1.5–2.0 μ wide. Asci long cylindrical to subclavate, abruptly to acutely and asymmetrically rounded at the tips, tapered from well above the middle to a long or short, fine stipe, 80–105 μ long, 5.0–7.5 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 60–85 μ long, 1.5–2 μ wide, incased in an inconspicuous, hyaline, gelatinous sheath.

Type locality: Lone Mountain, San Francisco, California.

Type specimen: Harkness, February, 1881. No. 2123.

Host: *Heteromeles arbutifolia:* California (Harkness, spec.).

Specimen examined: The type.

8. *Dermascia lacera* (Darker) n. comb.

Lophodermium lacerum Darker, Contrib. Arnold Arboretum Harvard Univ. 1 : 80. 1932.

Hysterothecia dull to shining black, hypophyllous, arranged in longitudinal rows on each side of the needle, broadly elliptical, 500–750 μ long by 280–400 μ wide, 150–250 μ deep; intraepidermal. Labia prominent, dark but not heavily carbonized, much thickened, 25–40 μ wide, opening widely and often torn by lateral cracks into several lobes, lined inwardly by a mass of hyaline periphyses 5–8 μ long by 1.5–2 μ wide. Basal layer a brown, translucent plate of pseudoparenchyma one to several cells thick which fills the lower halves of the epidermal cells, this overlaid to a thickness of 10–30 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover a well arched plate of dark brown or somewhat carbonized pseudoparenchyma 40–60 μ thick, often torn by cracks originating in the labia. Paraphyses hyaline, filamentous, simple, nonseptate, straight or flexuous, clavately enlarged at the tips, 110–125 μ long by about 1 μ wide, about equalling the asci and not gelatinized into an epithecium. Asci cylindrical to subclavate, asymmetrically rounded to subacute at the tips, tapered from above the middle to a broad base, 100–125 μ long, 12–16 μ wide, 8-spored. Ascospores filiform, hyaline, nonseptate, fasciculate and arranged in pairs, rounded at the tips and tapered to acute bases (clavate?), 60–85 μ long, 1.5–2.5 μ wide, incased in a conspicuous gelatinous matrix 3–4 μ thick.

Imperfect stage: Not named: An imperfect form was observed and described by Darker (1932) as having intraepidermal, black, subspherical pycnidia 120–170 μ long and 100–120 μ wide and hyaline, bacillar conidia 3–5 $\times$ 1–1.5 μ. The writer did not find this on the portion of the type specimen which he examined.

Type locality: Bear Island, Lake Timagami, Ontario, Canada.

Type specimen: G. D. Darker, No. 1459, June 16, 1925 (Arnold Arboretum Pathological Herbarium No. 820).

Host: *Abies balsamea:* New Hampshire, New York, Pennsylvania (Orton, spec.), Vermont, Ontario (Overholts and Parker, spec.), Quebec (Darker, 1932).

Illustrations: Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : pl. 22, figs. 1–6. 1932.

Specimens: C. R. Orton, Bear Meadows, Center Co., Pa., May 17, 1917; L. O. Overholts and C. S. Parker, Cochrane, Ont., Aug. 15, 1930.

Notes: The ascospores of this species were originally described as clavate. If this were strictly true, the species should have been referred

to Hypodermella. The ascospores are, however, filiform and only appear clavate because of their rounded tips and pointed bases. The gelatinous matrix in which they are incased is also thicker at the top than at the base and this tends to make the spores appear clavate.

9. *Dermascia latispora* n. sp.

Plate III, Figs. 5, 6.

Hysterothecia shining black, arranged in longitudinal rows in light stramineous, small or extensive spots on leaves and sheaths, elliptical with bluntly to sharply rounded ends, 500–750 μ long, 195–375 μ wide, intra-epidermal, in cross-section subspherical, in longitudinal section navicular, 200–225 μ deep. Labia well defined, thick, heavily carbonized, about two-thirds as long as the hysterothecia, spreading but little and exposing but a small part of the hymenium. Basal layer a brown, translucent plate 1 to 3 cells thick of pseudoparenchyma with an obvious radial disposition; this overlaid to a thickness of 10 μ by a closely interwoven, hyaline plectenchyma of very fine hyphae from which the hymenium arises. Cover carbonized at the margin and in the labia, elsewhere brown and translucent, consisting of flattened, crowded hyphae appearing to extend longitudinally in striae separated by walls of the epidermal cells. Paraphyses hyaline to dilutely yellow tinted, filamentous, straight or flexuous, somewhat clavately expanded at the tips and there united by gelatinization into a compact, orange-yellow epithecium 5–8 μ thick, 60–80 μ long by 1–1.5 μ wide. Asci broadly cylindrical to subclavate, asymmetrically rounded at the apex, tapered near the base to a broad, short stipe, 60–72 μ long, 12–15 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, straight, of uniform diameter, fasciculate and arranged in pairs, 52–66 μ long, 2–2.5 μ wide, gelatinous matrix inconspicuous.

Imperfect stage: Unknown.

Type locality: "Bei sulden am Ortler (Tyrol)." (Rehm, *exs.*)

Type specimen: Rehm, Ascomyceten No. 775.

Host: Gramineae.

Notes: In Rehm's exsiccati, this specimen was issued under the name *Lophodermium arundinaceum* f. *apiculatum* Duby but is distinct not only in its hysterothecial characters but in the characters presented by the asci and paraphyses. The ascospores are broader in this than in any other graminicole species, apparently have no tendency to become coiled in the ascus, and can be demonstrated with difficulty to possess a very thin and inconspicuous gelatinous matrix.

10. *Dermascia leptothecia* (Spegazzini) n. comb.

Plate V, Fig. 1.

Lophodermium leptothecium Spegazzini, Fungi Guaranitici I, No. 307. 1887. In Rev. Mycol. 9 : 89. 1887.

Hysterothecia dull to shining black, amphigenous, scattered in light stramineous areas of variable extent with very fine black, stromatic limiting lines, broadly oval, well arched with abruptly rounded ends, 350–600 μ long, 200–325 μ wide, occasionally confluent end to end, or laterally, so as to appear branched; intraepidermal. Labia carbonized, well arched, raised, becoming extroverted, cracked, and irregular in age, nearly as long as the hysterothecium, 15–25 μ wide, 20–30 μ thick, lined inwardly by gelatinous, hyaline, persistent periphyses. Cover well arched, carbonized in the region of the labia, elsewhere dark brown and more or less translucent, erose at the margins, thickened by the apposition, beneath, of 2 or more layers of dark brown pseudocollenchyma. Basal layer a plate one to several cells thick of dark brown, more or less translucent, noncarbonized, radiately arranged prosenchyma; this overlaid by a hyaline plectenchyma from which the hymenium arises. Paraphyses hyaline, filamentous, nonseptate, straight or flexuous, not clavately enlarged at the tips but variously crushed or bent and gelatinously agglutinated above to form a white epithecium 10–25 μ thick. Asci long-cylindrical to slenderly clavate, asymmetrically rounded above, tapered from above the middle to a long, fine stipe, 100 μ long, 4 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, straight or twisted with the ascus, 70–75 μ long, 0.75–1 μ wide.

Type locality: Guarapi, Paraguay.

Type specimen: B. Balansa, No. 3861, June, 1883. (Herbario Spegazzini, Museo de La Plata, No. 1009).

Host: *Laurinea:* Paraguay (Balansa, spec.).

Specimen examined: The type.

Note: Descriptive details relating to the hymenium are taken from Spegazzini's drawings and notes on the type specimen packet. In the specimen itself the hymenia have become disintegrated.

11. *Dermascia oxyasca* (Spegazzini) n. comb.

Plate V, Fig. 2.

Lophodermium oxyascum Spegazzini, Fungi Fuegiani No. 308. 1887. In Bol. Acad. Nac. Cien. Cordoba 11 : 135–311. 1887.

Hysterothecia dull or shining black, arranged in rows between sclerenchyma strands, widely spaced and without definite surrounding spots, elliptical with abruptly rounded to truncate ends, 600–700 μ long, 300–360 μ wide, intraepidermal. Labia prominent, well arched, heavily carbonized and opaque, tending to become extravert in age, 40–60 μ wide in the

middle, tapering toward the ends, 17–30 μ thick, lined inwardly by hyaline, clavately expanded, gelatinous and soon evanescent periphyses up to 25 μ long by 0.75–1 μ wide. Cover well arched, dark brown but translucent, carbonized in the region of the labia and at the erose margin, composed of one to several layers of pseudocollenchymatic cells. Basal layer a plate 1 to 4 cells thick of radiately disposed, dark brown, translucent prosenchyma, this overlaid to a depth of 12–15 μ by a finely interwoven, hyaline plectenchyma from which the hymenium arises. Paraphyses hyaline, filamentous, nonseptate, straight or flexuous, not clavately expanded but variously crushed and bent at the tips and forming a white epithecium up to 10 μ thick, 50–70 μ long, 1–1.5 μ wide. Asci cylindrical to subclavate, asymmetrically acute at the tips, tapered near the base to a short, broad stipe, 45–60 μ long, 5–6.5 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, straight or twisted with the ascus, 25–40 μ long, 0.75–1 μ wide, gelatinous matrix inconspicuous.

Type locality: Staten Island, Tierra del Fuego.

Type specimen: Herbario Spegazzini, No. 1004, in Museo de La Plata.

Host: *Gramineae* undetermined: Staten Island (Spegazzini, spec.).

Specimens examined: The type and a second specimen, Herbario Spegazzini No. 1005, without locality but bearing the note "Leg.? No. 6."

12. *Dermascia Reyesiana* (Rehm) n. comb.

Lophodermium Reyesianum Rehm, Leafl. Philippine Bot. 6 : 2233. 1914.

Hysterothecia minute, dull to shining black, amphigenous in darker or lighter discolored areas delimited by fine, black, stromatic lines, subrotund to oblong, with rounded ends, 200–315 μ wide by 250–730 μ long, intraepidermal. Labia nearly as long as the hysterothecium, of uniform width, heavily carbonized, raised, and tending to become extraverted with age, 10–20 μ wide, 10–15 μ thick, lined inwardly by a white mass of clavately expanded, septate, hyaline, gelatinized, persistent periphyses 6–15 μ long and 1.5–2 μ wide. Basal layer a dark brown, translucent plate one to several cells thick, composed of non-aliform, radiately disposed plectenchyma; this overlaid to a depth of 8–20 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover well arched, carbonized at the erose margin and in the labia but translucent brown in the intervening area, composed of a loosely interwoven plectenchyma of non-aliform hyphae. Paraphyses hyaline, filamentous, nonseptate, straight or flexuous, not clavately expanded but variously bent or crushed at the tips, gelatinously agglutinated above the asci into a shining white epithecium 5–10 μ thick, 90–105 μ long, 1–1.5 μ wide. Asci cylindrical to subclavate, asymmetrically and bluntly rounded above, tapered below to a fine, long stipe, 70–95 μ long,

5–6.5 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, straight or coiled within the ascus, fasciculate and arranged in pairs, 47–55 μ long, 1–1.5 μ wide, incased in an inconspicuous, hyaline, gelatinous matrix.

Imperfect stage: Unknown.

Type locality: Los Baños, Luzon.

Type specimen: C. F. Baker, No. 1585. Aug. 15, 1913. *Leg.* S. A. Reyes.

Host: On fallen, dead leaves: Philippine Islands (Rehm, 1914).

Specimen examined: Part of the type.

13. *Dermascia rotundata* (Sydow) n. comb.

Lophodermium rotundatum Sydow, Ann. Mycol. 12 : 201. 1914.

Hysterothecia dull to shining black, amphigenous in light brown spots up to 5 mm. in diameter and sharply marked off from the unoccupied tissue by a black stromatic line, subrotund to elongate and elliptical, 240–860 μ long, 200–300 μ wide, for the most part of the smaller sizes, intraepidermal. Labia well arched, 190–740 μ long, up to 70 μ wide, heavily carbonized, in the subrotund forms opening widely and cracking, lined inwardly by a white mass of gelatinous, clavately enlarged, soon evanescent, hyaline periphyses 10–20 μ long by 1–1.5 μ wide. Basal layer a brown, translucent, radiately constructed plate 1 cell thick; this overlaid to a depth of 5–10 μ by a closely interwoven, hyaline plectenchyma of very fine hyphae from which the hymenium arises. Cover well arched, heavily carbonized and nontranslucent, up to 50 μ thick, consisting of an outer carbonized region and an inner pseudocollenchymatic layer. Paraphyses hyaline, filamentous, simple, straight or slightly recurved at the tips, not expanded above and scarcely exceeding the asci in height, 60–90 μ long, 1 μ or less wide, epithecium indefinite or absent. Asci very slender, cylindric, asymmetrically and obtusely rounded at the tips, sessile and only slightly narrowed at the bases, 60–85 μ long, 4–6 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, straight or twisted with the ascus, fasciculate and arranged in pairs, 50–80 μ long, 0.75–1 μ wide, incased in a thin, inconspicuous gelatinous matrix.

Imperfect stage: Unknown.

Type locality: Mt. Maquiling, near Los Baños, Province of Laguna, Philippine Islands.

Type specimen: Baker, Fungi Malayana No. 39.

Hosts: Dilenia sp.: Philippines (Baker, exs., Sydow, 1914); Canarium sp.: Philippines (Baker, exs., 1931).

Exsiccati: Baker, Fungi Malayana Nos. 39 and 546.

Notes: According to Sydow (1914) this differs from *Lophodermium*

Mangiferae Koord. and *L. Canangae* Henn. & Nym. in its smaller, mostly rotund or short-elliptical hysterothecia. Aside, however, from the fact that it is intraepidermal, which distinguishes it from both these species, there are in some colonies very definitely elongated hysterothecia. Sydow's description says, "without spots," but the examples distributed by Baker are very definitely maculicole.

14. *Dermascia rubiicola* (Earle) n. comb.

Lophodermium rubiicolum Earle, Bul. Torrey Bot. Club 25 : 365. 1898.

Hysterothecia shining black, very abundant, crowded, and sometimes confluent end-to-end in unlimited, small to extensive, light stramineous areas on stems, broadly elliptical with rounded ends and erose margins, intraepidermal, 525–1200 μ long, 300–450 μ wide. Labia prominent, heavily carbonized, about $\frac{2}{3}$–$\frac{3}{4}$ as long as the hysterothecium, tending to become extroverted in age, 40–65 μ wide, up to 40 μ thick, lined inwardly by a white mass of gelatinizing and very soon evanescent, hyaline periphyses 8–12 μ long by 1–1.5 μ wide. Basal layer a dark brown, translucent plate 2 to several cells thick of non-aliform pseudoparenchyma; this overlaid to a depth of 15–25 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover well arched, erose at the margin in conformity with epidermal cells occupied, heavily carbonized except at the margin, consisting of a closely interwoven, plectenchyma of non-aliform hyphae. Paraphyses hyaline, non-septate, filamentous, straight or flexed, not clavately expanded but variously bent or crushed at the tips, 125–165 μ long, 0.75–1 μ wide, gelatinously coalesced above the asci in a white epithecium 20–35 μ thick. Asci cylindrical, abruptly and asymmetrically rounded above, tapered below to a fine, long stipe, 100–135 μ long, 5–6.5 μ wide, 8-spored. Ascospores hyaline, filiform, non-septate, acute at each end, fasciculate and arranged in pairs, straight or intricately coiled within the ascus, 75–95 μ long, 0.75–1 μ wide, incased in an inconspicuous, hyaline, gelatinous matrix.

Imperfect stage: Unknown.

Type locality: Auburn, Alabama.

Type specimen: Underwood and Earle, "Feb. & March, 1896." (In New York Botanical Garden).

Hosts: Rubus sp.:-Dead blackberry stems: Alabama (Earle, 1898, and specimen) ; dead stems of Rubus: California (H. E. Park, specimen).

Specimens examined: Underwood and Earle's type; H. E. Park, No. 2, Trinidad, California, May, 1931.

Notes: Earle's type specimen does not show, at the present time, the asci and spores described by Earle. The hymenia of the several

hysterothecia I examined had been invaded by a minute species of Penicillium and reduced to yellow masses of homogeneous, gelatinous material. The measurements given by Earle for the asci, 60–70 × 5 μ, are much less, as regards length, than those found in the California material. The fact that Earle noted in his description, yellow color in the ascospores and agglutinated paraphyses indicates that his specimen had already been invaded by the Penicillium and that the asci had not attained full development. Measurements of the asci and ascospores, given in the description above, are taken from the California specimen. For a discussion of *Lophodermium Rubi* (Pers.) Chev., which this species does not resemble in any way, see p. 115.

3. LOPHODERMELLINA von Höhnel (without description)

Berichte der Deutschen Botanischen Gesellschaft 35 : 419. 1917.

Ascomata in the form of hysterothecia, subrotund to elongate, flattened, immersed in the tissues of the host and inserted strictly within the epidermis, composed of separately developed bases and covers that are distinct at maturity and which possess plates of aliform mycelium forming the outer layer of the cover and the bottom layer of the base, opening by means of an elongated ostiole surrounded by more or less carbonized labia and lined with filiform, gelatinizing, persistent or evanescent periphyses. Hymenium consisting of both asci and paraphyses, disciform and strictly basal, arising from a closely interwoven, hyaline plectenchyma of fine hyphae. Paraphyses filamentous, nonseptate, and unbranched. Asci cylindrical, asymmetrically rounded above, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, incased in a gelatinous matrix.

Type species: *Lophodermellina hysterioides* (Persoon) von Höhnel, Ber. der Deutsch. Botan. Gesellsch. 35 : 422. 1917.

KEY TO THE SPECIES OF LOPHODERMELLINA

Asci generally more than 125 μ long; on Picea.................2. L. macrospora
Asci generally less than 125 μ long:
　Asci generally over 100 μ long:
　　Gelatinous matrix of ascospores conspicuous; on Abies and Picea..4. L. pinastri
　　Gelatinous matrix inconspicuous:
　　　Paraphyses clavately enlarged, on Psidium................7. L. subtropicalis
　　　Paraphyses not clavately enlarged, on Vincentia...............6. L. Stevensii
　Asci generally less than 100 μ long:
　　Ascospores 1.5–2 μ wide; on Sorbus............................9. L. tumida
　　Ascospores less than 1.5 μ wide:
　　　Epithecium yellow; on Rosaceae.......:...................1. L. hysterioides
　　　Epithecium white:
　　　　Asci slender, up to 6 μ wide; on Passiflora................3. L. Passiflorae
　　　　Asci broader, up to 10 μ wide:
　　　　　Paraphyses attenuated from base to tip; on Sesleria......5. L. Sesleriae
　　　　　Paraphyses clavately expanded above; on Triticum.........8. L. Tritici

1. *Lophodermellina hysterioides* (Persoon) von Höhnel

Xyloma hysterioides Persoon, Icon. et descrip. fung. p. 38, 1798 and Synopsis methodica fungorum, p. 106. 1801.
Hysterium Berberidis Schleicher, Plantae Crypt. Helvetiae Exs. No. 182. 1805.
Hypoderma xylomoides De Candole, Flore Française vol. 5, p. 164. 1815.
Hysterium foliicolum Fries, K. Vet. Akad. Handl. 40 : 102. 1819.
Hysterium foliicolum Fries, Systema mycologicum vol. 2 p. 592. 1823.
Lophodermium xylomoides Chevallier, Flore gén. des env. Paris, vol. 1, p. 437. 1826; Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 52. 1861.
Aporia microtheca Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 64. 1861.
Schizothyrium microthecum Saccardo, Sylloge fungorum 2 : 724. 1883.
Lophodermium hysterioides Saccardo, Sylloge fungorum 2 : 791. 1883.
Lophodermellina hysterioides von Höhnel, Ber. Deutsch. Bot. Gesellsch. 35 : 422. 1917 and Ann. Mycol. 15 : 311. 1917.

Hysterothecia shining black, in stramineous or light colored areas of very variable extent without black, stromatic lines on petioles, nerves, veinlets and blades of leaves, narrowly to broadly elliptical with rather acutely rounded ends, 650–1275 μ long, 330–500 μ wide, intraepidermal. Labia of the ostiole nearly as long as the hysterothecium, prominently raised at maturity, heavily carbonized, 20–35 μ wide, lined inwardly by a white mass of septate, cylindrical, gelatinously agglutinated and soon evanescent, hyaline periphyses up to 10 μ long and 1–1.5 μ wide. Basal layer a brown, translucent plate one cell thick of meandering, subradiately disposed aliform hyphae; this overlaid by a layer of closely interwoven, compact hyaline plectenchyma 10–20 μ thick from which the hymenium arises. Cover heavily carbonized throughout, consisting of an outer plate of aliform, meandering cells and, beneath this, a layer very variable in thickness of heavily carbonized pseudocollenchyma. Paraphyses filamentous, hyaline, straight or variously bent and crushed at the tips, not noticeably enlarged above, 85–100 μ long, about 1 μ wide, forming a thin but compact yellow-tinted epithecium. Asci cylindrical to subclavate, bluntly and asymmetrically rounded at the tips, tapering toward the base to a short, fine stipe, 80–100 μ long, 8–10 μ wide, 8-spored. Ascospores filiform, hyaline, nonseptate, straight or somewhat twisted with the ascus, fasciculate and arranged in pairs, 60–85 μ long, 0.75–1 μ wide, incased in a hyaline gelatinous matrix 1–1.5 μ thick.

Imperfect stage: Leptostroma maculicolum Hilitzer, Vĕdecké spisy vydáv. Českoslov. Akad. Zemĕd. 3 : 78. 1929.–Pycnidia intermixed with the hysterothecia, flat, opaque, 150–200 μ in diameter, 35–70 μ high; excipulum thin, its upper part one layer of brown pseudoparenchyma, its lower part of obscure plectenchyma; pore rounded, 5 μ in diameter. Conidiophores 15–18 μ long, bearing several spores on their somewhat attenuated tips. Conidia bacilliform, straight, nonseptate, 4–5 $\times$ 1 μ.

Type locality: Not given by Fries.

Type specimen: None specified; Fries (1823) cites Schleicher, Exsiccati Nos. 287 and 363.

Hosts: *Amelanchier alnifolia:* Washington (Ellis and Everhart, 1892); *A. ovalis:* Germany (Rehm, exs., 1925); *A. vulgaris:* Austria (Jaap, 1908); *Berberis* sp. (Rehm, 1887); *Crataegus* sp. (Rehm, 1887); *C. coccinea:* England (Berkeley, exs.), Germany (Jaap, 1914); *C. monogyma:* France (Roumeguère, exs.); *Pyrus* sp. (Rehm, 1887); *P. communis:* Serbia (Ranojevic, 1910), Thuringia (Sydow, exs.).

Exsiccati: Berkeley, British Fungi No. 196; Rabenhorst, Fungi europaei No. 1151; Rehm, Ascomyceten No. 1323b; Roumeguère, Fungi sel. Gallici exs. No. 551; Sydow, Mycoth. Germ. No. 493.

The following, which I have not seen, are cited by Rehm (1887) Fuckel, Fungi rhen. No. 742; Mougeot et Nestler, Stirp. Crypt. No. 761 *sub Xyloma umbilicatum* Pers.; Rabenhorst, Herb. myc. II, No. 156; Rehm, Ascomyceten No. 867.

Illustrations: Killian et Likhité, Compt. rend. hebdomad. des seances et mém. Soc. Biologie 1924 2 : 575, figs. 1–15. 1924. Persoon, Icon. et descr. fung. pl. 10, figs. 3, 4. 1798.

Note: The fungus distributed in Rabenhorst's Fungi europaei No. 3869 as *Lophodermium hysterioides* is not, at least in the copy available to me, that species. The ascomata are very broadly oval to subcircular, amphigenous, and scattered over the blade more than the rib or petiole. The host probably is not Pyrus, as given; and this record of *L. hysterioides* on Pyrus sp. in Sardinia should be deleted. The specimen appears immature. There are no asci and the ascomata have not opened.

2. *Lophodermellina macrospora* (Hartig) n. comb.

Plate III, Fig. 7.

Hysterium macrosporum Hartig, Wichtige Krankheiten der Waldbaume, p. 101. 1874.

Hypodermella macrospora Lagerberg, Medd. Stats. Skogsforsoksant. 7 : 113. 1910.

Lophodermium macrosporum Rehm, Rabenhorst's Kryptogamen Flora vol. 3, p. 45. 1887.

Hysterothecia dull to shining black, on the outer faces of needles, 400–650 μ wide, variable in length and extending at times almost the entire length of the needle, intraepidermal. Labia well carbonized and conspicuous, up to 85 μ wide, nearly as long as the hysterothecium, opening widely and exposing much of the orange tinted hymenium. Basal layer a brown, translucent plate 1 cell thick of aliform, radiately disposed hyphae; this covered to a depth of 20–30 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover carbonized near the margins and in the labia but not elsewhere, composed of an outer layer of meandering aliform hyphae and,

beneath this, of a brown pseudocollenchyma, 50–70 μ thick. Paraphyses orange tinted above, straight or variously curved, not expanded above, filamentous, 100–160 μ long, united above in a thick, orange epithecium. Asci cylindrical to subclavate, abruptly and asymmetrically subacute at the tip, tapered near the base to a broad stipe, 100–150 μ long, 14–20 μ wide, 8-spored. Ascospores filiform to subclavate, rounded above, tapered to a fine point below, hyaline, continuous, fasciculate and arranged in pairs until the asci elongate, 50–80 μ long, 2–3 μ wide, incased in a conspicuous, hyaline gelatinous sheath 2–4 μ thick.

Imperfect stage: Hypodermina Hartigii Hilitzer, Vĕdeké spisy vydáv. Českoslov. Akad. Zeměd. 3 : 57. 1929.–*Vide* Hartig, 1874.

Type locality: Treves, Germany.

Type specimen: Not specified.

Host: *Picea Abies:* Czechoslovakia (Darker, 1932; Hilitzer, 1929, Picbauer, 1932) ; Denmark (Darker, 1932) ; France (de Thuemen, exs.) ; Germany (Hartig, 1874; Jaap, 1914; Krieger, exs., Rabenhorst, exs.) ; Norway (Darker, 1932) ; Poland (Krieger, exs.) ; Sweden (Darker, 1932), Switzerland (Darker, 1932, Kunze, exs.).

Exsiccati: Krieger, Schadliche Pilze: 2 specimens, without number, designated (1) Prebischtor 25.4.1910, 16.6.1897 and (2) juni 1909, both leg. Krieger; Kunze, Fungi sel. exs. No. 374 (Fungi Helv. No. 74) ; de Thuemen, Nycoth. univ. No. 279.

Rehm (1887) also cites: Rabenhorst, Fungi europ. No. 2411 and de Thuemen, Fungi Austr. 1157. Darker (1932) cites: Krieger, Fungi Sax. No. 777; Petrack, Fl. Boh. and Morav. exs. II ser. No. 2052; and Siemaszko, Fungi Bialow. exs. No. 16.

Illustrations: Hartig, Wichtige Krankheiten der Waldbaume, pl. 6, figs. 1–17. 1874; Hilitzer, Vĕdecké spisy vydáv. Českoslov. Akad. Zeměd. 3 : pl. 4, fig. 17. 1929; Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : pl. 25, fig. 4. 1932.

3. *Lophodermellina Passiflorae* (Rehm) n. comb.

Plate III, Fig. 8.

Lophodermium Passiflorae Rehm, Leafl. Philippine Bot. 6 : 2232. 1914.

Hysterothecia dull black, scattered in extensive, light brown, unlimited and poorly defined areas on stems, oval to long elliptical, occasionally confluent, 400–900 μ long, 200–350 μ wide, intraepidermal. Labia pronounced and heavily carbonized, 275–750 μ long, 20–30 μ wide, lined inwardly with a white or yellow mass of hyaline, gelatinous and soon evanescent periphyses 15–25 μ long by 1–1.5 μ wide. Basal layer a light brown, translucent plate 1 cell thick consisting of a radiately arranged prosenchyma, the marginal cells of which are distinctly aliform;

this covered to a depth of 20 μ by a hyaline, closely interwoven plectenchyma of fine hyphae from which the hymenium arises. Cover carbonized at the margins and in the labia, light brown and translucent between these, consisting of a loosely compacted layer of aliform plectenchyma which straggles out from the margins into the host tissue; this underlaid in the region of the labia by several layers of heavily thickened pseudocollenchymatous cells. Paraphyses hyaline, filamentous, straight or crushed at the tips by pressure, not clavately expanded, 90–125 μ long, 1 μ wide, united above into a firm, white epithecium. Asci cylindrical to subclavate, bluntly and asymmetrically rounded at the tips, tapered toward the base into a short, thin stipe, 65–90 μ long, 4.5–6 μ wide, 8-spored. Ascospores hyaline, filamentous, straight or somewhat twisted with the ascus, nonseptate, 55–80 μ long, 0.75–1 μ wide, gelatinous matrix very inconspicuous.

Imperfect stage: Unknown.

Type locality: Mt. Maquiling, near Los Baños, Province of Laguna, Philippine Islands.

Host: *Passiflora quadrangularis:* Philippines (Rehm, 1914; Baker, exs., 1914).

Exsiccati: Baker, Fungi Malayana No. 38.

Notes: This species, as represented in the set of Baker's exsiccati available to the writer, is deceptive. Of the 10 pieces of stem in the packet, only 2 bear the fungus, the others being attacked by a variety of other fungi. While the hysterothecia are intraepidermal, the aliform nature of their structure is masked to a very considerable extent by the heavy carbonization of the hysterothecial margins and by the tendency, throughout the cover, for the very slightly chytinized fungous cells to occupy areas corresponding to the top halves of the host's epidermal cells. When the host tissue has been sufficiently bleached, however, irregular extensions of the marginal hyphae furnish the typical aliform structure.

4. *Lophodermellina pinastri* (Chevallier) von Höhnel

Plate III, Figs. 9–11.

Hysterium pinastri Schrader, Schrad. Journ. Bot. 2 : 69. 1799, in part.
Hysterium limitatum Wiebel, Prim. Fl. Werth., p. 329. 1799, in part.
Hypoderma pinastri De Candolle, Flore Française, 3rd Ed., vol. 5, p. 305, 1815, in part.
Hysterium pinastri Fries, K. Vet. Akad. Handl. 40 : 101. 1819, in part.
Hysterium pinastri Fries, Systema Mycologicum, vol. 2, p. 587, 1823, in part.
Hypodermium sparsum Link, Species plantarum, 4 Ed., vol. 6; p. 88. 1824, in part.
Lophodermium pinastri Chevallier, Flore gén. des env. de Paris, vol. 1, p. 436. 1826.
Aporia obscura Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 63. 1861, in part.

Depazea linearis Rostrup, Tidsskr. Skovbr. 6 : 260. 1883, in part.
Phacidium Piceae Fuckel, Symbolae Mycologicae, Nacht. II, p. 51. 1873.
Schizothyrium obscurum Saccardo, Sylloge fungorum 2 : 725. 1883, in part.
Coccomyces Piceae Saccardo, Sylloge fungorum 8 : 746. 1889.
Lophodermium Abietis Rostrup, Tidsskr. Skovbr. 12 : 201. 1891.
Lophodermium Piceae von Höhnel, Sitzungsb. K. Akad. Wissensch. Wien (Math.-
    Nat. Kl.) 126 : 296. 1917.
Lophodermellina pinastri von Höhnel, Ann. Mycol. 15 : 311. 1917.

Hysterothecia dull or shining black, in longitudinal rows on either side of the middle ridge of the outer faces of needles, the area occupied by each cut off from adjacent areas by a heavy black, stromatic line which extends across the needle and along which the needle breaks readily, 950–2200 μ long, 450–700 μ wide, elliptical to linear with abruptly rounded ends, intraepidermal. Labia usually heavily carbonized, poorly defined, up to 50 μ wide, lined inwardly by a white mass of gelatinous, clavately enlarged, hyaline periphyses 15–25 μ long and 1–1.5 μ wide. Basal layer a brown, translucent plate 1 to 3 cells thick, consisting of radiately arranged, aliform prosenchyma; this overlaid to a depth of about 5 μ by a closely interwoven, hyaline prosenchyma of very fine hyphae from which the hymenium arises. Cover well arched, carbonized at the margins, very heavily carbonized in the region of the labia, varying from translucent to opaque and carbonized in the intervening area, distinctly aliform in structure. Paraphyses filamentous, straight or flexuous, clavately enlarged at the tips and there incased in a gelatinous matrix by which they are bound together above the asci in a dense white epithecium about 10 μ thick, 90–140 μ long, 0.75–1 μ wide. Asci long-cylindrical to subclavate, asymmetrically acute or subacute at the tips, somewhat tapered below to a broad base, 90–130 μ long, 8–12 μ wide, 8-spored. Ascospores filiform, hyaline, straight or intricately coiled within the ascus, fasciculate and arranged in pairs, nonseptate, 85–115 μ long, 1.5–2 μ wide, incased in a gelatinous matrix up to 2 μ thick.

Imperfect stage: Hypodermina Abietis (Dearness) Hilitzer, Vĕdecké spisy vydáv. Českoslov. Akad. Zemĕd. 3 : 60. 1929. (*Leptostroma Abietis* Dearness, N. Y. St. Museum Bul. 266 : 65. 1925).–Pycnidia intraepidermal, dark brown, 200–435 μ long, 125–200 μ wide; exciple aliform. Ostiole about 25 μ wide, substomatal. Conidiophores 15–22 μ long, 1 μ wide. Conidia elliptical to oblong, hyaline, straight or subarcuate, 3–4 × 0.5–0.8 μ.

Type locality: Malmedy, Belgium.

Type specimen: Roumeguère, Fungi Gall. exs. No. 1661.

Hosts: *Abies alba:* Denmark (Rostrup, 1891; Lind. 1913); *A. balsamea:* Ontario (Darker, 1932); *A. concolor:* Oregon (Darker, 1932); *A. lasiocarpa:* Oregon (Darker, 1932); *Picea Abies:* Massachu-

setts and Oregon (Darker, 1932), Denmark (Rostrup, 1891; Lind, 1913), Belgium (Roumeguère, exs.), Germany (von Höhnel, 1917; Jaap, 1914); *P. glauca:* Michigan, Ontario, and Quebec (Darker, 1932), Denmark (Rostrup, 1891; Lind, 1913); *P. Engelmanii:* Oregon (Darker, 1932); *P. mariana:* Ontario and Quebec (Darker, 1932); *P. rubra:* New York (Darker, 1932); *P. sitchensis:* California and Oregon (Darker, 1932), Denmark (Rostrup, 1891; Lind, 1913), Scotland (Darker, 1932). See also Jaap (1914), Sydow, *et al.* (1911), and Hilitzer (1929).

Exsiccati: Roumeguère, Fungi Gall. exs. No. 1661; de Thuemen, Fungi Austr. No. 1059; Fuckel, Fungi rehn. No. 2561.

Illustrations: Rostrup, Tidsskr. Skovbr. 12 : 201, fig. 3; 203, fig. 4b. 1891; Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : pl. 1, fig. 3; pl. 23, figs. 1–11; pl. 24, figs. 1–11; pl. 25, figs. 1–3. 1932.

The treatment given this species by Darker (1932) appears to have been based on a misconception of the type. Following the studies of von Tubeuf (1901, 1910), Haack (1911), Lagerberg (1914), and Hagem (1928), he has limited the species to the genus Pinus, as to hosts, upon which he finds it to be widely distributed throughout the northern hemisphere. In this, it is assumed that *Lophodermium pinastri* Chevallier is in all respects synonymous with *Hysterium pinastri* Schrader; but this assumption is not justified. Though Chevallier (1826) probably considered the two to be synonymous, the material with which he dealt was on *Picea Abies.* What purports to be type material is to be found in Roumeguère's Fungi Gallici exsiccati, No. 1661, under the following label:

> 1661. Lophodermium pinastri (Schrad.) Chev. Fl. Paris.   .
> (Type)
> Sur les Aiguilles des Pins.
> Malmedy   (Reliq. Libertianae)

If, as seems likely, this specimen is part of the material with which Chevallier dealt, it should be held to typify the species and should not be confused with material cited by Schrader, Fries, or others. The Roumeguère specimen is not on pine, but on Picea and, from our determination, on *P. Abies* Karst. This is, of course, not contrary to Chevallier's original description, in which the host of the fungus is stated to be *"pin sauvage,"* for which the common meaning is not necessarily restricted to the genus Pinus but may extend also to other evergreens.

This fungus, on Picea and Abies, was recognized as a species distinct from the *Lophodermium pinastri* of Schrader and Fries by Fuckel (1873), by Rostrup (1891), and by von Höhnel (1917); and von Höhnel transferred it to his new genus Lophodermellina (1917). According to Darker (1932), von Höhnel's material was all *L. Piceae.* Hence, it appears that von Höhnel has rightly interpreted the species.

The report by Lind (1913) of this species on Pseudotsuga has been shown by Boyce (1928) to be erroneous. This and certain other hosts listed by Hilitzer (1929) are taken directly from Lind and should be interpreted in the light of Boyce's report.

5. *Lophodermellina Sesleriae* (Hilitzer) n. comb.

Lophodermium Sesleriae Hilitzer, Vědecké spisy vydáv. Českoslov. Akad. Zeměd. 3 : 91. 1929.

Hysterothecia shining black, scattered in light stramineous, unlimited spots on leaves, sheaths, and culms, elliptical to oblong, always attenuated at the ends and appearing almost fusiform, 700–1000 μ long, 200–600 μ wide, intraepidermal. Labia indistinct, poorly differentiated, up to 35 μ wide, lined inwardly by hyaline periphyses up to 10 μ long. Basal layer a brown, translucent plate one cell thick of radiately disposed, aliform hyphae, this overlaid to a depth of 10–15 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover more or less carbonized, consisting of an outer plate of radiately disposed, aliform hyphae, thickened by the apposition beneath of brown pseudocollenchyma to a depth of 15–25 μ. Paraphyses hyaline, filamentous, straight or flexuous, about equalling the asci, not clavately expanded above and not forming an epithecium, 80–100 μ long, 2 μ wide at the base, 1 μ wide at the tips. Asci cylindrical to subclavate, asymmetrically subacute at the tips, tapered below to a long, thin stipe, 75–100 μ long, 9 μ wide, 8-spored. Ascospores hyaline, nonseptate, filiform, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 55–75 μ long, 1–1.5 μ wide, incased in an inconspicuous, hyaline, gelatinous matrix about 1 μ thick.

Imperfect stage: Unknown.

Type locality: Not specified by Hilitzer.

Type specimen: Not designated by Hilitzer.

Host: *Sesleria coerulea:* Central Bohemia (Hilitzer, 1929), Germany, Italy, Switzerland (Hilitzer, 1929).

6. *Lophodermellina Stevensii* n. sp.

Hysterothecia dull black, amphigenous, scattered in light stramineous areas of variable extent on blades of dead leaves, elliptical to linear with abruptly rounded ends and erose margins, 475–1150 μ long, 200–315 μ wide, intraepidermal, arranged without reference to the directions of the veins of the host. Labia prominent, extroverted and cracking away with age, nearly as long as the hysterothecia, very heavily carbonized, of uniform width throughout their length, up to 55 μ wide, 30 μ thick, lined

on the inner edges by hyaline, clavately expanded, gelatinizing and very soon evanescent periphyses 8–15 μ long by 1.5–2 μ wide. Basal layer a plate 2 to several cells thick, consisting of dark brown, translucent pseudoparenchyma without evident radiate distribution but distinctly aliform at the margin; this overlaid to a depth of 8–20 μ by a closely interwoven, hyaline, fine plectenchyma from which the hymenium arises. Cover a loosely to compactly interwoven plate of brown, translucent, aliform, hyphae, non-carbonized except in the labia and at the erose margin. Paraphyses hyaline, straight or flexuous, very slightly or not at all enlarged at the tips but interwoven there into a dense, gelatinously compacted epithecium up to 30 μ thick, 100–130 μ long by 1 μ thick. Asci long cylindrical, asymmetrically conical and subacute at the apex, gradually tapered from well above the middle to a fine, long stipe, 90–110 μ long, 5–7 μ wide, 8-spored. Ascospores hyaline, nonseptate, straight or coiled once in the upper part of the ascus, fasciculate and arranged in pairs, somewhat tapered at each end, about 75 μ long and 1–1.5 μ wide, gelatinous matrix very thin and inconspicuous.

Imperfect stage: Unknown.

Type locality: Mt. Olympus, Island of Oahu, Hawaii.

Type specimen: Stevens, Hawaiian Fungi No. 727.

Host: *Vincentia angustifolia:* Hawaii (Stevens, 1925, and in exs.).

Exsiccati: Stevens, Hawaiian Fungi Nos. 246, 373, 622, 652, and 727.

7. *Lophodermellina subtropicalis* (Spegazzini) n. comb.

Plate V, Fig. 3.

Lophodermium subtropicale Spegazzini, Anal. Museo Nac. Buenos Aires 23 : 88. 1912.

Hysterothecia dull black, oriented parallel with the stem axis in longitudinally extensive, cinereous areas sharply delimited by fine, black, stromatic lines, narrowly elliptical with indeterminate margins and ends, 1200–2100 μ long, 500–750 μ wide, intraepidermal. Labia indistinct, carbonized and opaque, bordered inwardly by a gelatinous mass of deliquesced periphyses. Cover heavily carbonized and opaque except at the margin, there extending to a distance of 250 μ or more beyond the margin of the base and filling the epidermal cells with loose wefts of dark brown, translucent, aliformly terminated hyphae. Basal layer an indefinite plate, hyaline and translucent in the middle, dark brown to opaque at the margins; this overlaid by a closely interwoven hyaline plectenchyma from which the hymenium·arises. Paraphyses filamentous, hyaline, straight or flexuous, markedly clavately enlarged at the tips which are gelatinously agglutinated above the asci into a shining white epithecium 5 to 8 μ thick, 120–160 μ long, 1–1.5 μ wide. Asci long

cylindrical to subclavate, asymmetrically acute at the tips, tapered from about the middle to a long, slender stipe, 100–150 μ long, 6.5–8 μ wide, 8-spored. Ascospores filiform, hyaline, non-septate, fasciculate and arranged in pairs, straight or coiled within the ascus, 70–100 μ long, 1–1.5 μ wide, incased in a thin and inconspicuous, hyaline, gelatinous sheath.

Type locality: Puerto Leon, Misiones, Argentina.

Type specimen: Herbario Spegazzini No. 1008, September 1909.

Host: *Psidium* sp. : Argentina (Spegazzini, spec.).

Specimen examined: The type.

8. *Lophodermellina Tritici* (Roumeguère) n. comb.

Plate III, Fig. 13.

Lophodermium arundinaceum f. *Tritici* Roumeguère, Fungi selecti exsiccati No. 6144, 1892, and Rev. Mycol. 14 : 168. 1892.

Hysterothecia shining black, in longitudinal rows between veins in extensive, light stramineous spots on sheaths and stems, elliptical to oblong, pointed at the ends, 650–1500 μ long, 300–450 μ wide, mostly of the larger sizes, intraepidermal. Labia heavily carbonized, well arched, 30–35 μ wide, at least ¾ the length of the hysterothecium, lined inwardly with a white mass of filiform, nonseptate, gelatinized, hyaline periphyses 10–20 μ long. Basal layer a brown, translucent plate one cell thick composed of radiately arranged aliform hyphae. Cover well arched, carbonized heavily in the region of the labia and the margin, the intervening area less heavily carbonized and underlaid with several layers of brown pseudocollenchymatous cells, the outer layer definitely aliform and radial in disposition. Paraphyses hyaline, filamentous, straight or flexuous, clavately expanded for some distance at the tips and gelatinously fused into a white epithecium 10–15 μ thick, 70–100 μ long, 1–1.5 μ wide. Asci cylindrical to subclavate, asymmetrically rounded to subacute at the tips, tapered from near the base to a short, broad stipe, 55–90 μ long, 6.5–11 μ wide, 8-spored. Ascospores hyaline, nonseptate, filiform, straight or somewhat twisted with the ascus, fasciculate and arranged in pairs, of uniform diameter, 45–80 μ long by about 1 μ wide, incased in a thin and inconspicuous gelatinous matrix.

Imperfect stage: Unknown.

Type locality: Not stated; presumably France.

Type specimen: Roumeguère, Fungi selecti exsiccati No. 6144.

Hosts: *Triticum hibernum:* France? (Roumeguère, exs.) ; *T. vulgare:* Ohio (Ellis and Everhart, 1892), Pennsylvania (Fulton, spec.), Italy (de Thuemen, exs.).

Exsiccati: Roumeguère, Fungi selecti exsiccati No. 6144; de Thuemen, Mycoth. univ. No. 661.

Specimen: H. R. Fulton, State College, Pa., May 23, 1908.

9. *Lophodermellina tumida* (Fries) von Höhnel

Hysterium tumidum Fries, Systema Mycologicum vol. 2, p. 591. 1823.
Coccomyces tumida Fuckel, Symbolae mycologici, p. 257, 1869. Not de Notaris,
   Giorn. Bot. Ital. 2 : 38. 1847.
Lophodermium tumidum Rehm, Rabenhorst's Kryptogamen Flora, vol. 3, p. 40.
   1887.
Lophodermellina tumida von Höhnel, Ann. Mycol. 15 : 312. 1917.

Hysterothecia shining black, scattered and frequently crowded and contiguous in stramineous spots without black stromatic borders on leaves, very broadly elliptical, abruptly rounded at the ends, 420–1500 μ long, 300–1000 μ wide, intraepidermal. Labia heavily carbonized, about ⅔ as long as the hysterothecium, 35–45 μ wide, up to 80 μ thick, lined inwardly by a white mass of short, septate, clavately enlarged, gelatinous and soon evanescent, hyaline periphyses 10–15 μ long and 2 μ wide. Basal layer a light brown, translucent plate 1 cell thick, composed of aliform, elongated, radially disposed cells. Cover usually heavily carbonized throughout, composed of an outer plate of aliform, radiately disposed but more or less meandering cells and, beneath this,· a layer of pseudocollenchymatous cells 30–50 μ thick; the cover often breaking away entirely. Paraphyses hyaline, filamentous, straight or variously bent or crushed by pressure at the tips, not clavately enlarged, not exceeding the asci and forming no epithecium, 80–90 μ long, uniformly 2 μ wide. Asci cylindrical to broadly clavate, asymmetrically subacute at the tips, tapered below to a rather broad base, 70-90 μ long, 8–10 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 40–60 μ long, 2–2.5 μ wide, incased in a conspicuous gelatinous sheath 1.5–2 μ thick.

Imperfect stage: Leptostroma sorbicolum Hilitzer, Vědecké spisy vydáv. Československ. Akad. Zeměd. 3 : 80. 1929.–Pycnidia minute, black, shining, 200–400 μ in diameter, with a thin excipulum of 1 or 2 layers of brown, aliform hyphae; ostiole up to 7 μ in diameter. Conidiophores sparingly branched, 10–15 μ long, 2 μ wide, bearing several spores at the apex. Conidia bacillar, straight, nonseptate, hyaline, 3–5 × 1 μ.

Type locality: Not given by Fries.

Type specimen: Fries, Scleromyceti Sueciae exsiccati No. 166.

Hosts: *Sorbus Aucuparia:* Switzerland and Austria (Rehm, 1887), Czechoslovakia (Hilitzer, 1929) ; *S. americana:* New Brunswick, Canada (Farlow, exs.).

Exsiccati: Rehm, Ascomyceten No. 519; Fuckel, Fungi rhen. No. 746; Reliquiae Farlow. No. 51.

Notes: Rehm (1887, p. 40) distinguished the variety Napelli, for which he gives as host *Aconitum Napellus*. I have not been able to see material of this, but supposed that it should be considered a separate species. Rehm describes the asci as being 105 μ long and the spores as 60–75 $\times$ 1.25 μ. Chevallier (1826) records *Lophodermium herbarum* on this host.

4. LOPHODERMINA von Höhnel (without description)

Berichte der Deutschen Botanischen Gesellschaft 35 : 418. 1917.

Ascomata in the form of hysterothecia, subrotund to elongate, flattened, immersed in the tissues of the host and inserted strictly between cuticle and epidermis, composed of separately developed bases and covers that are distinct at maturity and which possess plates of aliform mycelium forming the outer layer of the cover and the bottom layer of the base. Opening an elongated ostiole surrounded by thickened and more or less carbonized labia and lined with filiform, gelatinizing, persistent or evanescent periphyses. Hymenium consisting of both asci and paraphyses, disciform and strictly basal, arising from a closely interwoven, hyaline plectenchyma of fine hyphae. Paraphyses filamentous, nonseptate, unbranched. Asci cylindrical, asymmetrically rounded above, 4- or 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, incased in a more or less conspicuous hyaline gelatinous sheath.

Type species: *Lophodermina melaleuca* (Fries) von Höhnel, Ber. der Deutsch. Botan. Gesellsch. 35 : 422. 1917, and Ann. Mycol. 15 : 312. 1917.

KEY TO THE SPECIES OF LOPHODERMINA

Asci generally more than 125 μ long:
  Ascospores septate...21. L. septata
  Ascospores not septate in the ascus:
    Periphyses, in mass, and epithecium yellow; on Pinus...........7. L. conigena
    Periphyses, in mass, and epithecium white; on Abies..........4. L. autumnalis
Asci generally less than 125 μ long:
  Asci generally 100 μ or more long:
    Asci 4-spored; on Thuya....................................22. L. Thuyae
  Asci 8-spored:
    Ascospores 2 μ or more wide:
      Asci broad, up to 18 μ wide; on Juniperus...............11. L. juniperina
      Asci slenderer, not over 14 μ wide:
        On Pinus...15. L. nitens
        On Rhododendron...............................20. L. Rhododendri
    Ascospores 1.5–2 μ wide:
      Gelatinous matrix 3–4 μ thick; on Abies..................23. L. uncinata
      Gelatinous matrix about 1 μ thick:
        Periphyses white in mass; on Larix.....................12. L. laricina
        Periphyses yellow in mass; on Pernetia.................6. L. clavuligera

Asci generally less than 100 μ long:
  Ascospores broad, generally more than 1.5 μ wide:
    Ascospores very broad, 2 μ or more wide; on Chamaedaphne..16. L. orbicularis
    Ascospores more slender, 1.5–2 μ wide:
      Periphyses, in mass, and epithecium yellow; on Vaccinium...14. L. melaleuca
      Periphyses, in mass, and epithecium white:
        Periphyses slender, 1–1.5 μ wide; on Marsipospermum......2. L. antarctica
        Periphyses coarser, 2–2.5 μ wide; on Vaccinium..........13. L. macularis
  Ascospores more slender, generally less than 1.5 μ wide:
    Ascospores 1–1.5 μ wide:
      Periphyses, in mass, and epithecium yellow; on Gramineae...3. L. apiculata
      Periphyses, in mass, and epithecium white; on
        Quercus, etc.....................................19. L. punctiformis
    Ascospores very slender, 1 μ or less wide:
      Periphyses, in mass, and epithecium yellow:
        Paraphyses clavately expanded; ascospores 45 μ or more long;
          on Epilobium..5. L. ciliata
        Paraphyses not clavately expanded; ascospores less than 45 μ
          long; on Salix....................................24. L. versicolor
      Periphyses, in mass, or epithecium white
        Paraphyses clavately expanded; on Cupressus....9. L. Cupressi-thyoidis
        Paraphyses not clavately expanded:
          Paraphyses longer than the asci, forming an epithecium: •
          Asci generally less than 50 μ long; on Kalmia........10. L. exarida
          Asci generally more than 50 μ long:
            Asci broad, up to 9 μ wide; on Aira..............8. L. culmigena
            Asci slender, up to 6 μ wide; on Planchonia.........1. L. Aleuritis
         Paraphyses about equalling the asci, epithecium indefinite or absent:
          Asci generally more than 50 μ long; on Prunus......18. L. prunicola
          Asci generally less than 50 μ long; on Paeonia......17. L. Paeoniae

1. *Lophodermina Aleuritis* (Rehm) n. comb.

Plate IV, Figs. 13–15.

Lophodermium Aleuritis Rehm, Leafl. Philippine Bot. 6 : 2232. 1914.
Lophodermium Planchoniae Rehm, Leafl. Philippine Bot. 8 : 2925. 1914.

Hysterothecia shining black, amphigenous and scattered in light stramineous, extensive, irregular spots 2–4 mm. in diameter and delimited by fine, black, stromatic lines, short to long elliptical or linear, straight or curved and lunate, 375–600 μ long, 180–350 μ wide, subcuticular. Labia heavily carbonized, tending to become extroverted, nearly as long as the hysterothecia, 20–35 μ wide; lined inwardly by a shining white mass of gelatinizing, clavately enlarged, persistent periphyses 5–15 μ long and 1–1.5 μ wide. Basal layer a brown, translucent plate one cell thick, sometimes thickened toward the middle by the apposition, above, of one or two layers of pseudoparenchyma, consisting of radiately disposed aliform plectenchyma; this overlaid to a depth of 5–20 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover carbonized and opaque in the region of the labia, elsewhere brown and more or less translucent, consisting of an outer plate of heavily chytinized, radiately disposed, aliform hyphae

which extend at the margin to a distance of 10–50 μ beyond the margin of the base, this thickened by the apposition, beneath, of several layers of pseudocollenchymatous cells.   Paraphyses hyaline, filamentous, straight or flexuous, not clavately expanded above but variously bent or crushed by pressure and gelatinously coalesced into a shining white epithecium 10–12 μ thick, 80–110 μ long, 0.75–1 μ wide.   Asci cylindrical to subclavate, asymmetrically and bluntly rounded above, tapered from below the middle to a broad stipe, 60–80 μ long, 4.5–6 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, twisted or intricately coiled within the ascus, 45–70 μ long, 0.75–1 μ wide, incased in an inconspicuous gelatinous matrix.

Imperfect stage: Unknown.

Type locality: Mount Maquiling, near Los Baños, Province of Laguna, Philippine Islands.

Type specimen: C. F. Baker No. 2076. Luzon, Prov. Laguna. 11/1913. *Leg.* S. A. Reyes.

Hosts: *Aleurites moluccana:* Philippine Islands (Rehm, 1914) ; *Planchonia spectabilis:* Philippine Islands (Rehm, 1916; Baker, 1931, exs.) ; dead leaves: Philippine Islands (Rehm, 1914; Baker, 1931, exs.).

Exsiccati: Baker, Fungi Malayana, Nos. 154, 156.

Note: The specimen labeled *Lophodermium Aleuritis* Rehm in Baker's exsiccatum, No. 154, is identical in all respects, even to host, with *L. Planchoniae.* Baker's exsiccatum No. 154 gives the host only as "dead leaves." Since the species name, *Aleuritis,* has precedence because of earlier publication, I have chosen to reduce the later name to synonymy, though realizing the danger of a misconception of the host relationship.

2. *Lophodermina antarctica* (Spegazzini) n. comb.

Plate V, Fig. 4.

Lophodermium antarcticum Spegazzini, Fungi Fuegiani No. 304. 1887. In Bol. Acad. Nac. Cienc. Cordoba 11 : 135-311. 1887.

Hysterothecia shining black, arranged with the long axis parallel with the stem axis, scattered in small, poorly defined, not delimited, light stramineous areas on stems, broadly elliptical to subrotund, 660–940 μ long, 375–625 μ wide, subcuticular.   Labia indistinct, much arched but not extroverted, heavily carbonized and opaque, 50–70 μ wide in the center, tapering towards both ends, up to 35 μ thick, lined inwardly at first by a white mass of hyaline, gelatinously agglutinating and very soon evanescent, clavately expanded periphyses 6–10 μ long by 1–1.5 μ wide.   Cover hemispherical, carbonized and opaque except at the margin, which extends as a loosely constructed, erose skirt of brown, prosenchymatic, aliformly terminated hyphae to a distance of 40 to 70 μ beyond the base.   Basal layer a plate one cell thick of dark brown, radiately

disposed, aliform prosenchyma; this overlaid to a depth of 5 to 12 μ by a closely interwoven, hyaline plectenchyma from which the hymenium arises.   Paraphyses filamentous, hyaline, straight or flexuous, not clavately expanded but variously crushed and bent at the tips and gelatinously agglutinated above the asci into a white epithecium 10–20 μ thick, 70–100 μ long, 1–1.5 μ wide. Asci cylindrical, asymmetrical and abruptly rounded to truncate at the tips, tapered near the base to a short, broad stipe, 65–80 μ long, 8–10 μ wide, 8-spored. Ascospores filiform, hyaline, nonseptate, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 45–60 μ long, 1.5–2 μ wide, incased in a conspicuous, hyaline, gelatinous sheath 1.2–2 μ thick.

Type locality: Staten Island, Tierra del Fuego.

Type specimen: No. 1010 in Herbario Spegazzini, Museo de La Plata.

Host: *Marsipospermum* sp. : Staten Island, Tierra del Fuego (Spegazzini, spec.).

Specimen examined: The type.

3. *Lophodermina apiculata* (Wormsk. *ex* Fries) n. comb.

Plate IV, Fig. 7.

Hysterium apiculatum Wormsk. ex Fries, Systema Mycologicum, vol. 2, p. 593. 1823.
Lophodermium arundinaceum γ *apiculatum* Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 59. 1861.
Lophodermium apiculatum Duby, in Saccardo, Sylloge Fungorum 2 : 797. 1883.
Lophodermium arundinaceum f. *apiculatum* Rehm, in Rabenhorst's Kryptogamen Flora, vol. 3, p. 46. 1887.
Hysterium Actinothyrium Fuckel, Symbolae Mycologicae, Nacht. III, p. 28, 1877.
Lophodermium arundinaceum var. *Actinothyrium* Rehm, in Rabenhorst's Kryptogamen Flora, vol. 3, p. 47. 1887.

Hysterothecia dull black, scattered in light stramineous spots of various extent in arid leaves, arranged in rows between and oriented parallel with veins, broadly to narrowly elliptical, often with ends pointed and extended subcuticularly into tapered and acute mycelial mucrons, 225–750 μ long, 210–300 μ wide, subcuticular. Labia prominent, heavily carbonized, up to 35 μ wide, 15–35 μ thick, turning outward and at first presenting a shining white mass of periphyses, these soon evanescent, gelatinously agglutinated, 2–3 μ wide and 15–25 μ long. Basal layer about 1 cell thick (2–3 cells thick at the margins), composed of pseudoparenchymatous, brown, translucent hyphae aliform at the margins; this overlaid to a depth of 5–10 μ by a finely interwoven layer of hyaline plectenchyma. Cover somewhat carbonized at the margins, elsewhere brown and more or less translucent, not apparently aliform except at the margin, where definitely aliform cells mark the edge of the cover. Paraphyses filamentous, straight or variously bent and crushed at the tips,

somewhat swollen and club-shaped at the tips, and united by gelatinization into a heavy, shining-white to yellowish epithecium about 5 μ thick, about 1 μ wide, up to 85 μ long. Asci cylindrical, obtuse to subacute and asymmetrical at the tips, somewhat tapered from below the middle to a short, narrow stipe, 45–80 μ long, 6.5–10 μ wide, 8-spored. Ascospores filiform, hyaline, non-septate, fasciculate and arranged in pairs, 40–75 μ long, 1–1.5 μ wide, incased in a thin, hyaline, gelatinous matrix, sometimes straight but usually with one marked twist near the top of the ascus.

Imperfect stage: Actinothyrium graminis Kunze, according to Rehm (1887). Spores filiform, curved, hyaline, 50×1 μ.

Type locality: Kamchatka (Fries, 1823).

Type specimen: Not specified; Fries cites no specimen.

Hosts: Undetermined grasses: Kamchatka (Fries, 1823); *Calamagrostis arundinacea:* Czechoslovakia (Hilitzer, 1929), Germany (Sydow, *exs.*); *C. sylvaticum:* Germany (de Thuemen, *exs.*); *C. epigeios:* Czechoslovakia (Hilitzer, 1929); *C. villosa:* Czechoslovakia (Hilitzer, 1929); *C. canadensis:* Colorado (Clements *exs.*); *Molinia coerulea:* Germany (Rehm, 1896; Sydow, *exs.,* Switzerland (Kunze, *exs.*).

Exsiccati: Kunze, Fungi selecti No. 372; de Thuemen, Mycoth. univ. No. 471; Rehm, Ascomyceten No. 775; Sydow, Mycoth. germ. No. 81, No. 897; Clements, Crypt. Format. Colo. No. 48.

Illustrations: Corda, Icones Fungorum vol. 5, pl. 9, fig. 58. 1842.

Remarks: The distinction upon which this species was based is the remarkable, tapering, pointed ends of the hysterothecia. This, however, is a character not uniformly developed, and is to be found in various degrees of development or may be entirely absent, both on Calamagrostis and on *Molinea coerulea*. Fries (1823) notes, " . . *sed distinctissimum mucrone, qui vero in junioribus non distinguitur"* but in the material that we have examined even completely mature and empty hysterothecia lack the apical points while others, taken only a few millimeters away on the same host material, possess it to a very marked extent. It is present on both host genera, and since the fungi on the two hosts are not distinct otherwise, we have united the two species under the earlier name.

4. *Lophodermina autumnalis* (Darker) n. comb.

Plate I, Fig. 9.

Lophodermium autumnale Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : 77. 1932.

Hysterothecia shining black, occurring on needles primarily attacked by nervisequious Hypodermataceae, scattered or crowded and frequently becoming confluent, elliptical, 400–800 μ long, 270–420 μ wide, 150–300 μ

deep, subcuticular. Labia indefinite, not greatly thickened or markedly carbonized, lined inwardly by a white mass of filiform, clavately expanded, soon evanescent, hyaline periphyses up to 20 μ long and 1.5–2 μ wide. Basal layer a very loosely compacted plate of radiately disposed brown, translucent, aliform, meandering prosenchyma; this overlaid to a depth of 15–25 μ by a closely interwoven, columnar, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover well arched, brown and more or less translucent, composed of an outer plate of heavily chytinized, meandering, aliform hyphae which extend outward at the margin to as much as 20 μ beyond the margin of the base, this thickened by the apposition beneath of pseudocollenchyma to a thickness of 50 μ in the region of the labia. Paraphyses hyaline, filamentous, straight or flexuous, very slightly clavately expanded at the tips, 130–160 μ long, not exceeding the asci in length and forming no epithecium, about 1 μ wide. Asci cylindrical to subclavate, asymmetrically subacute at the tips, tapered to a rather broad, short stipe, 110–160 μ long, 12–15 μ wide; 8-spored. Ascospores filiform, hyaline, nonseptate, straight or somewhat twisted with the ascus, fasciculate and arranged in pairs, 80–100 μ long, 1.5–2 μ wide, incased in a gelatinous matrix 3–5 μ thick.

Imperfect stage: Unknown.

Type locality: Claude Lake, Gaspe County, Quebec, Canada.

Type specimen: J. H. Faull, No. 8748, collected Sept. 1928.

Hosts: *Abies amabilis:* Oregon (Darker, 1932); *A. balsamea:* Michigan, Nova Scotia, Ontario, and Quebec (Darker, 1932); *A. concolor:* California (Boyce, spec.), Oregon (Darker, 1932); *A. lasiocarpa:* Idaho (Darker, 1932), Utah (Korstian, spec.), Wyoming (Weir, No. 9169; Sydow and Petrak, 1922); *A. magnifica:* California (Boyce, spec.); *A. nobilis;* Oregon (Darker, 1932).

Specimens: Boyce, Weaver Bally Mt., Cal., June 22, 1914; Korstian, Ephraim, Utah, Sept. 4, 1918; Boyce, Hyampton, Cal., June 12, 1914.

Illustrations: Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : pl. 21, figs. 1–5. 1932.

5. *Lophodermina ciliata* (Libert) n. comb.

Hysterium ciliatum Libert, in herb., according to Roumeguère and Saccardo, Rev. Mycol. 3 : 39. 1881.
Lophodermium ciliatum Spegazzini and Roumeguère, Rev. Mycol. 3 : 39. 1881.

Hysterothecia dull to shining black, scattered in dead, stramineous areas on stems, very broadly oval, 450–825 μ long, 225–475 μ wide, subcuticular. Labia carbonized, becoming extroverted, nearly as long as the hysterothecia, 20–40 μ wide, lined inwardly by a yellow mass of gelatinous, clavately expanded, persistent periphyses up to 25 μ long and

1–1.5 μ wide. Basal layer a brown, translucent plate of radiately disposed, aliform hyphae thickened in the middle by the apposition, above, of about three layers of brown pseudoparenchyma; this overlaid to a depth of 10–30 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover well rounded, carbonized in the vicinity of the labia, elsewhere more or less translucent, consisting of an outer plate of radiately disposed aliform mycelium thickened by the apposition, beneath, of several layers of pseudocollenchymatous cells. Paraphyses hyaline, filamentous, straight or flexuous, clavately expanded at the tips and there incased in a gelatinous sheath by which they are agglutinated into a thick, firm, orange-yellow epithecium, 50–90 μ long, 0.75–1 μ wide. Asci narrowly cylindrical to subclavate, asymmetrically subacute at the tips, tapered from below the middle to a fine stipe, 50–80 μ long, 6–8 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 45–70 μ long, 0.75–1 μ wide, gelatinous matrix inconspicuous.

Imperfect stage: Unknown.

Type locality: Malmedy, Belgium.

Type specimen: Roumeguère, Fungi Selecti Gallici Exsiccati No. 662.

Host: *Epilobium angustifolium:* Belgium (Roumeguère, exs.).

Exsiccati: Roumeguère, Fungi sel. Gall. exs. No. 662, "Add caules *Epilobii angustifolii,* prope Malmedyanum, Vere *Reliquiae Libertianae.*"

Notes: The type specimen, as distributed by Roumeguère and available to me, is in very poor condition, the shape of the hysterothecia, their mycelial structure, and rarely an ascus with paraphyses, being all that is visible. The original diagnosis cannot be greatly improved upon, though it is evident that the marginal cilia required in that description are only the epidermal hairs of the host.

6. *Lophodermina clavuligera* (Spegazzini) n. comb.

Plate V, Fig. 6.

Lophodermium clavuligerum Speg., Fungi. Fuegiani No. 305. 1887. In Bol. Acad. Nac. Cienc. Cordoba 11 : 135–311. 1887.

Hysterothecia dull black, amphigenous, in indistinct areas delimited by black, stromatic lines, broadly elliptical to subrotund, with rounded ends, 500–850 μ long, 400–625 μ wide, subcuticular. Labia indistinct and but little raised, not extroverted in age, 25–50 μ wide, 15–20 μ thick, lined inwardly by a yellow mass of clavate, short, gelatinous and very soon evanescent periphyses 6–12 μ long by 1.5–2 μ wide. Cover somewhat arched, carbonized in the region of the labia, elsewhere dark brown and somewhat translucent, composed of an outer plate of meandering,

aliform mycelium underlaid by brown pseudocollenchyma. Basal layer a plate of brown, radiately disposed, meandering aliform prosenchyma thickened, upward, by the apposition of one or two layers of brown pseudoparenchyma; this overlaid to a depth of 12–18 μ by a closely interwoven, yellowish plectenchyma of fine hyphae from which the hymenium arises. Paraphyses filamentous, yellow in mass, straight or flexuous, clavately expanded at the tips and agglutinated about the ascus-tips into a thin, readily dissolved, yellow epithecium. Asci cylindrical to slightly clavate, bluntly and asymmetrically round above, tapered from the middle to a broad base, 100–110 μ long, 6–7.5 μ wide, 8-spored. Ascospores hyaline, filiform, septate, yellow-tinted in mass, straight or twisted with the ascus, 85–100 μ long, 1–1.5 μ wide, gelatinous matrix inconspicuous.

Type locality: Staten Island, Tierra del Fuego.

Type specimen: "Herbario Spegazzini" No. 1006 (Museo de la Plata).

Host: *Pernettia mucronata* : Staten Island (Spegazzini, spec.).

Specimen examined: The type.

Notes: The type specimen, which is the only record of this fungus that I have been able to find, is very scant. It consists of 4 small host leaves with a few hysterothecia on each. Characters of the hymenium are no longer determinable; but on the packet containing the specimen Spegazzini has made his characteristically fine, pencil drawings showing the shape of the paraphyses, asci, and spores, dimensions being noted for each of these structures. The items indicated by his drawings and notes furnish the material upon which the above description of paraphyses, asci, and spores is based.

7. *Lophodermina conigena* (Brunaud) n. comb.

Lophodermium pinastri f. *conigena* P. Brunaud, Act. de la Soc. Linn. de Bordeaux 42 : 97. 1888.
Lophodermium conigenum Hilitzer, Vědecké spisy vydáv. Českoslov. Akad. Zeměd. 3 : 76. 1929.

Hysterothecia shining black, irregularly scattered over scales of cones, elliptical with obtusely rounded ends, 1500–2000 μ long, 800–1000 μ wide, subcuticular. Labia narrow, eventually extroverted, heavily carbonized, 70–100 μ wide, up to 45 μ thick, lined inwardly with a yellow mass of gelatinizing, more or less persistent, clavately expanded periphyses 15–35 μ long and 1.5–2 μ wide. Basal layer a dark brown, more or less translucent plate of radiately disposed aliform plectenchyma thickened by the apposition, above, of one to several layers of brown pseudoparenchyma; this overlaid to a depth of 25 μ by a closely interwoven,

hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover carbonized near the margins and in the region of the labia, in the intervening area more or less translucent, consisting of an outer plate of radiately disposed aliform plectenchyma thickened by the apposition to varying depths of brown pseudocollenchyma, extending outward at the margin 5–30 μ beyond the margin of the base. Paraphyses hyaline, filamentous, straight or flexuous, not clavately expanded but bent and crushed at the tips, 150–200 μ long, about 1.5 μ wide, gelatinously agglutinated above the asci and forming a white epithecium up to 20 μ thick. Asci cylindrical to long-clavate, asymmetrically conical and obtuse at the tips, tapered to a broad stipe, 130–180 μ long, 12–14 μ wide, 8-spored. Ascospores filiform, hyaline, nonseptate, fasciculate and arranged in pairs, straight or coiled in the ascus, 100–150 μ long, 1.5–2 μ wide, incased in a hyaline, gelatinous matrix 1.5–2 μ thick.

Imperfect stage: Unknown.

Type locality: Not given by Brunaud.

Type specimens: Not designated by Brunaud.

Hosts: Pinus sylvestris: France (Brunaud, 1888); P. uliginosa: Czechoslovakia (Hilitzer, 1929).

Illustrations: Hilitzer, Vědecké spisy vydáv. Českoslov. Akad. Zeměd. 3 : pl. 4, fig. 18. 1929.

8. Lophodermina culmigena (Fries) von Höhnel

Plate IV, Figs. 1–4.

Hysterium culmigenum Fries, K. Vet. Akad. Handl. 38 : 96. 1817; Observ. mycol. praecip. ad illustr. floram Suec., pt. 2, p. 355. 1818; Systema Mycologicum, vol. 2, p. 591. 1823.

Lophodermium arundinaceum δ culmigenum Fuckel, Jahrb. d. Nassauischen Ver. f. Naturk. 23/24 : 257. 1869/70.

Lophodermium culmigenum Karsten, Ofvers. af Kongl. Vetensk.-Akad. Forh. 2 : No. 28. 1872.

Lophodermina culmigena von Höhnel, Ann. Mycol. 15 : 313. 1917.

Hysterothecia dull to shining black, in light stramineous extensive areas on culms, sheaths, and leaves, arranged in rows between and oriented parallel with veins and strands of sclerenchyma, narrowly to broadly elliptical with truncate ends from which cylindrical hyphae straggle out loosely between epidermis and cuticle, 450–1100 μ long, 225–400 μ wide, subcuticular. Labia prominent, heavily carbonized, 50–70 μ wide, up to 60 μ thick, extroverted in age, lined inwardly with a white mass of clavately expanded, gelatinous and soon evanescent, hyaline periphyses 10–18 μ long by 1–1.5 μ wide. Basal layer a brown, translucent plate of radiately disposed aliform prosenchyma thickened toward the middle by the apposition, above, of two to four layers of

brown pseudoparenchyma; this overlaid to a depth of 10–35 μ by a closely interwoven hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover tending to become heavily carbonized with age, consisting of an outer plate of heavily chytinized aliform mycelium which extends outward at the margin 10–50 μ beyond the margin of the base and is aliformly terminated along the sides but not at the ends of the hysterothecium. Paraphyses hyaline, filiform, straight or flexuous, not clavately expanded and but little crushed or bent by pressure, 50–100 μ long, gelatinously coalesced at the tips into a thin, fragile, easily dissolved, white epithecium. Asci cylindrical to subclavate, asymmetrically subacute at the tips, somewhat tapered near the base to a short, broad stipe, 45–90 μ long, 5–9 μ wide, 8-spored. Ascospores hyaline, nonseptate, filiform, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 45–75 μ long, 1 μ wide, incased in a more or less conspicuous gelatinous matrix up to 1.5 μ thick.

Imperfect stage: Unknown.

Type locality: Not given by Fries.

Type specimen: Not specified; Fries (1823) cites Scleromyceti Sueciae exsiccati No. 97.

Hosts: *Elymus arenarius* (Fries, 1823); *Aira flexuosa:* Sweden (?Fries, 1823), Kamchatka (?Fries, 1823); Germany (Sydow, exs.), France (Roumeguère, exs.).

Exsiccati: Roumeguère, Fungi sel. exs. No. 7043; Sydow, Mycoth. Germ. Nos. 1599, 2147.

Illustrations: Fries, Observ. mycol. praecip. ad illustr. floram Suec., pt. 2, pl. 7, fig. 3. 1818.

9. *Lophodermina Cupressi-thyoidis* (Saccardo) n. comb.

Lophodermium juniperinum f. *Cupressi-thyoidis* Saccardo, Michelia 2 : 570. 1882.

Hysterothecia shining black, on scale leaves at the tips of dead twigs, elliptical, with ends rounded, 450–650 μ long, 270–330 μ wide, subcuticular, placed on one or the other side of the central nerve of the scale, usually only one on each scale, rarely two. Labia poorly defined and very little carbonized, not greatly thickened and distinguishable only by sectioning, ⅔–¾ the length of the hysterothecium, not opening widely, lined within by a white mass of gelatinizing, soon evanescent, hyaline periphyses 5–12 μ long, 1–1.5 μ wide. Basal layer a brown, translucent plate one cell thick of radiately disposed aliform prosenchyma; this overlaid to a depth of but 1–3 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover but very little carbonized, brown and translucent, consisting of an outer plate of dichotomous, aliform plectenchyma thickened by the apposition beneath

of one to several layers of slightly colored pseudoparenchyma, extending 10–20 μ beyond the margin of the base. Paraphyses hyaline, filamentous, straight or flexuous, simple, clavately expanded at the tips and there gelatinously coalesced in a thin, hyaline epithecium, 50–95 μ long, 1.5–2 μ wide. Asci cylindric to subclavate, asymmetrically subacute or rounded at the tips, tapering from below the middle to a very fine stipe, 65–90 μ long, 6.5–8 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 44–60 μ long, 0.75–1 μ wide, incased in a hyaline, gelatinous matrix 1–1.5 μ wide.

Imperfect stage: Unknown.

Type locality: Newfield, New Jersey.

Type specimen: Ellis, North American Fungi No. 999 b.

Host: *Chamaecyparis thyoides:* New Jersey (Ellis, exs., 1892).

Exsiccati: Ellis, North American Fungi No. 999 b. (type).

Notes: Darker (1932) has, apparently following Saccardo, included this fungus under *Lophodermium juniperinum.* He lists Saccardo's name for it as a synonym, and in his host list gives *Chamaecyparis thyoides* in New Jersey. Presumably this is on the authority of either Ellis and Everhart (1892) or Saccardo (1882), as there is no indication in his list of exsiccati or specimens examined that he has seen the Ellis specimen, which is, of course, to be regarded as the type upon which Saccardo based his name.

Upon comparison of actual material, there seems to be no reason for regarding the forms on Juniperus and Chamaecyparis as identical, or even as variants of the same species. While both are subcuticular in location with respect to the host and very definitely composed outwardly of aliform mycelium, they have in other ways decided differences. The most easily observed of these is the contrast in carbonization and thickening of the hysterothecia and hysterothecial labia. In the form on Chamaecyparis, the asci fail by 20 μ of reaching the shortest of those on Juniperus, the spores are neither so long nor so wide, the asci not so wide, and the paraphyses far less wide.

10. *Lophodermina exarida* (Cooke & Peck) n. comb.

Hysterium exaridum Cooke & Peck, Twenty-ninth Report, N. Y. State Museum, 1875: 63. 1878, and Cook & Peck, Bull. Buffalo Soc. Nat. Sci., 1875: pt. 3, p. 36. 1875.
Lophodermium exaridum Saccardo, Sylloge Fungorum, vol. 2, p. 792. 1883.

Hysterothecia shining black, amphigenous and usually within 1–2 mm. of the margins of extensive, brown, irregular spots sharply delimited by very fine, black, stromatic lines, elliptical, 270–825 μ long, 210–425 μ

wide, subcuticular. Labia prominent, well arched, extroverted at maturity, carbonized through about ½ their length at their middles, almost as long as the hysterothecia, 35–60 μ wide, lined inwardly by a white mass of hyaline, clavately expanded, gelatinously agglutinated periphyses 5–12 μ long by about 1 μ wide. Basal layer a brown, translucent plate one cell thick, consisting of radiately disposed aliform prosenchyma, this overlaid to a depth of 2–5 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover but little carbonized, consisting of an outer plate of chytinized, translucent, aliform mycelium thickened variably by the apposition, beneath, of pseudoparenchymatous cells. Paraphyses hyaline, filamentous, straight or flexuous, not clavately enlarged but much bent and crushed by pressure and gelatinously united into a very thin (3 μ thick) white epithecium, 35–50 μ long, 0.75–1 μ wide. Asci cylindrical to subclavate, asymmetrically rounded or abruptly subacute at the tips, tapered from above the middle to a fine stipe, 35–50 μ long, 6–9 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, 33–40 μ long, 0.75–1 μ wide, incased in a hyaline, gelatinous matrix 1–1.5 μ thick.

Imperfect stage: Unknown.

Type locality: Not given by Peck (1878).

Type specimen: Not cited by Peck (1878).

Hosts: *Kalmia angustifolia:* New York (Cooke 1875, Peck 1878), New Hampshire: (Farlow, exs.) ; *Kalmia latifolia:* New Jersey (Ellis, exs., 1892).

Exsiccati: Ellis, North Am. Fungi No. 998; Reliquiae Farlowianae No. 47.

11. *Lophodermina juniperina* (Fries) n. comb.

Plate II, Fig. 6; Plate III, Fig. 14; Plate IV, Figs. 5, 6.

Hysterium juniperinum Fries, Observ. mycol. praecip. ad illustr. floram Suec., pt. 2, p. 355. 1818.
Hysterium pinastri β juniperinum Fries, Systema mycologicum vol. 2, p. 588. 1823.
Hysterium Juniperi Greville, Scottish Cryptogamic Flora, vol. 1, pl. 26. 1823.
Lophodermium juniperinum de Notaris, Giorn. Bot. Ital. 2 : 6. 1847.
Lophodermium Sabinae Fautrey, Rev. Mycol. 13 : 169. 1891.

Hysterothecia shining black, scattered, amphigenous but especially on the upper faces of leaves, elliptical, often truncate at the ends, 350–900 μ long, 250–450 μ wide, 150–170 μ high, subcuticular. Labia on most hosts and in old material much thickened and carbonized, on some hosts (*Juniperus communis*) hardly differentiated, lined inwardly by a white mass of clavately enlarged, gelatinizing and soon evanescent periphyses 7–15 μ long, 1.5–2 μ thick. Basal layer a light brown, translucent plate one cell thick of radiately disposed, dichotomously divided aliform plectenchyma; this overlaid to a depth of 5–10 μ by a closely interwoven,

hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover brown and translucent to heavily carbonized and opaque, consisting of an outer, dichotomous, aliform plate heavily chytinized and extending at the margin as much as 30 μ beyond the margin of the base, thickened to as much as 50 μ by the apposition, beneath, of pseudocollenchymatous cells. Paraphyses hyaline, filiform, much bent at the tips by pressure, clavately expanded at the tips, agglutinated above the asci into a compact, white epithecium 10–20 μ thick, up to 150 μ long, 1.5 μ wide. Asci cylindrical to subclavate, asymmetrically acute to subacute at the tips, tapered from somewhat above the middle to a broad or fine stipe, 100–130 μ long; 10–17 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, of uniform diameter, fasciculate and arranged in pairs, often multiguttulate, 60–100 μ long, 2–3 μ wide, incased in a conspicuous, hyaline, gelatinous matrix up to 3 μ thick.

Imperfect stage: Unknown.

Type locality: Not given by Fries.

Type specimen: Not cited by Fries.

Hosts: *Chamaecyparis* sp. : Germany (Darker, 1932) ; *Juniperus* sp. : Ireland (Greville, 1823) ; *J. chinensis* var. *Sargenti:* Massachusetts (Darker, 1932) ; *J. communis:* Colorado (Clements, exs.), Iowa (Ellis & Everhart, 1892), Michigan (Hansen, spec.), New York, Washington, and Maine (Darker, 1932), Austria (de Thuemen, exs.), Belgium (Darker, 1932), Czechoslovakia (Hilitzer, 1929), England (Berkeley, exs.), France (Roumeguère, exs.), Germany (Jaap, 1914; Sydow, exs.), Italy (de Notaris, 1847), Scotland (Greville, 1823), Switzerland (Jaap, 1907) ; var. *depressa:* Maine, Massachusetts, New Hampshire, and Ontario (Darker, 1932) ; *J. horizontalis:* Massachusetts, Ontario (Darker, 1932) ; *J. Sabina:* Denmark (Lind, 1913), France, Poland, Switzerland (Darker, 1932), Germany (Jaap, 1916) ; *J. squamata:* Denmark (Lind, 1913) ; *J. oxycedrus:* Austria (Jaap, 1916) ; *J. virginiana:* Massachusetts, New York, Ontario (Darker, 1932), Denmark (Lind, 1913). *Libocedrus decurrens:* California (Darker, 1932), Oregon (Darker, 1932; Zeller, 1927).

Exsiccati: Clements, Crypt. Format. Colo. No. 50; Ellis, N. Am. Fungi No. 999 a; Krypt, exsic. ed. u Museo Palat. Vindob. No. 2220; Rehm, Ascomyceten No. 128; Roumeguère, Fungi Gall. sel. exs. No. 1870; Roumeguère, Fungi. sel. exs. No. 5863; Reliquiae Farlowianae (Fungi) No. 48; Sydow, Mycoth. Germ. No. 1600; de Thuemen, Fungi austriaci No. 1268; de Thuemen Mycoth. univ. No. 76.

Specimen: A. A. Hansen, Calumet, Mich., Aug. 8, 1916.

Illustrations: Greville, Scott. Crypt. Flora, vol. 1, pl. 26, figs. 1–4. 1823; Hilitzer, Vědecké spisy vydáv. Českoslov. Akad. Zeměd. 3 : 15,

fig. 4. 1929; Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : pl. 17, figs. 1–7. 1932.

Notes: In No. 3545 of Roumeguère's Fungi Gallici exsiccati, distributed as *Lophodermium juniperinum* f. *minor* Roumeguère on leaves of *Juniperus communis,* the package available to us contains a grass (Panicum sp.) upon which no Lophodermium is present. The validity of the form could not be determined.

12. *Lophodermina laricina* (Duby) n. comb.

Lophodermium laricinum Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 58, 1861.

Hysterothecia shining black, occurring singly or in pairs in sections of needles delimited by black, stromatic lines along which the needles break readily, amphigenous, subcuticular, elliptical, well arched, 450–680 μ long, 210–430 μ wide, subcuticular. Basal layer a brown, translucent plate one to three cells thick of compact, radially disposed aliform prosenchyma; this overlaid to a depth of 15–30 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover a plate of dark brown, heavily chytinized and nearly opaque, dichotomously branched aliform hyphae thickened by the apposition, beneath, to a depth of 20–50 μ of pseudocollenchymatous cells. Labia strongly carbonized, 80–85 μ wide, up to 450 μ long, up to 50 μ thick, lined inwardly by a white mass of clavately expanded, gelatinizing and soon evanescent hyaline periphyses 12–30 μ long and 1–1.5 μ wide. Paraphyses hyaline, filamentous, straight or flexuous, not clavately expanded, much bent and crushed at the tips by pressure but not exceeding the asci in height and forming no epithecium, 100–120 μ long, 1–1.5 μ wide. Asci cylindrical to subclavate, asymmetrically blunt or subacute at the tips, tapered very slightly to a broad base, 95–135 μ long, 12–15 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, straight or intricately coiled within the ascus, fasciculate and arranged in pairs, 85–130 μ long, 1.5–2 μ wide, incased in a hyaline, gelatinous sheath about 1 μ thick.

Imperfect form: *Leptostroma laricinum* Fuckel, Jarhb. d. Nassauischen Ver. f. Naturk. 23/24 : 256. 1869/70. Pycnidia subcuticular, the cover and base of very fine aliform mycelium, round to elliptic, brown, translucent, 110–200 μ long by 80–160 μ, shining black. Conidia hyaline, nonseptate, bacilliform, 4–5 μ long, 0.5–1 μ wide.

Type locality: *"Ad radices orientales Alpium Pedemontii,"* as stated by Duby (1861).

Type specimen: Not designated. ·

Hosts: *Larix* sp. : Japan (Shirai and Hara, 1927), Austria (Jaap, 1916); *L. decidua:* Austria (Jaap, 1916), Italy (Saccardo, exs.), Switzerland (Darker, 1932); *L. laricina:* Ontario, Quebec (Darker, 1932).

Exsiccati: Fuckel, Fungi rhen. No. 743; Rabenhorst, Fungi europ. No. 158; Rehm, Ascomyceten, No. 1751; Saccardo, Mycoth. Ital. No. 505. The imperfect form is exemplified in Fuckel, Fungi rhen. No. 196 and Sydow, Mycoth. March. No. 4768.

Illustration: Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : pl. 20, figs. 4–9. 1932; von Tubeuf, Arb. Biol. Abth. Forst.-u. Landw. Kaiserl. Gesundh. 2 : pl. 3, figs. 11–19. 1901.

13. *Lophodermina macularis* (Fries) n. comb.

Plate IV, Figs. 8–11.

Hysterium maculare Fries, Systema Mycologicum, vol. 2, p. 592. 1823.
Lophodermium maculare de Notaris, Giorn. Bot. Ital. 2 : 40. 1847.
?*Lophodermium maculare* var. *albolabrum* Ellis and Everhart, The North American Pyrenomycetes, p. 859. 1892.
Lophodermium maculare var. *Arctostapyli* Rehm, Ber. Bayer. Bot. Gesellsch. 13 : 16. 1912.

Hysterothecia dull or shining black, amphigenous, solitary or several in white, irregularly angular, papery spots delimited very sharply from the surrounding brown leaf tissue by fine black, stromatic lines, nearly circular to broadly elliptical with rounded ends, well arched, 345–700 × 230–420 μ, subcuticular. Labia prominent and becoming extroverted, about ¾ the length of the hysterothecium, heavily carbonized, 30–50 μ wide, lined inwardly by a prominent, white mass of filiform, clavately expanded, nonseptate, gelatinously agglutinated, hyaline periphyses 20–30 μ long and 2–2.5 μ wide. Cover well arched, more or less translucent, thin at the edges, up to 50 μ thick at the labia, consisting of an outer plate of dichotomously branched aliform hyphae thickened by the apposition, below, of subcarbonaceous pseudocollenchyma. Basal layer a brown, translucent plate one to three cells thick of radiately disposed plectenchyma, the outer layer aliform; this overlaid to a depth of 10–15 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Paraphyses hyaline, filamentous, straight or flexuous, bent by pressure at the tips but not enlarged or swollen, gelatinously agglutinated and forming a dense, white epithecium up to 25 μ thick, 90–135 μ long, 1–1.5 μ wide. Asci cylindrical, bluntly and asymmetrically rounded at the tips, tapered near the base to a short, narrow stipe, 60 × 9 to 120 × 14 μ, 8-spored. Ascospores hyaline, filiform, nonseptate, of uniform diameter, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 55–95 μ long, 1.5–2 μ wide, incased in a hyaline, gelatinous matrix 1–1.5 μ thick.

Imperfect stage: Unknown.

Type locality: Not given by Fries.

Type specimen: Fries, Scleromyceti Sueciae exsiccati No. 167.

Hosts: *Arctostaphylos* sp. : Oregon (Zeller, sp.) ; *A. uva-ursae:* Germany (Rehm, 1912) ; "Quaking Ash" : Utah (Ellis, exs.) ; *Vaccinium ovatum:* Oregon (Zeller, 1927) ; *V. pennsylvanicum* (de Thuemen, exs.) ; *V. uliginosum:* Germany and France (Duby, 1861), Sweden (Fries, 1823).

Exsiccati: Ellis, North Amer. Fungi. No. 859; Roumeguère, Fungi selecti Gallici No. 553; Sydow, Mycoth. German. No. 2146; de Thuemen, Mycoth. univ. No. 75.–Rehm (1887) also cites Fuckel, Fungi rhen. No. 1752, and Mougeot & Nestler, Stirp. Crypt. No. 1072.

Specimen: S. M. Zeller, Rhododendron, Ore., July 6, 1929. No. 8989.

Notes: The example distributed in Ravanel's Fungi americani exsiccati, No. 179, on Quercus sp. (Q. Phellos L.?) is not a Lophodermina. The hysterothecia are intraepidermal and possess decidedly clavate, long stalked asci. The spores are 1-celled, somewhat curved, hyaline, 17–20 × 4–4.5 μ. The specimen is referable to Hypoderma.

Ellis and Everhart's variety *albolabrum,* based on the "Quaking Ash" specimen, is not different from the species. They did not distinguish correctly between *L. macularis,* which has white periphyses, and *L. melaleucum,* which has yellow periphyses.

14. *Lophodermina melaleuca* (Fries) von Höhnel

Hysterium melaleucum Fries, Observ. mycol. praecip. ad illustr. floram Suec., pt. 1,
   p. 192. 1815; K. Vet. Akad. Handl. 40 : 96. 1819; Systema Mycologicum, vol.
   2, p. 589. 1823.
B *Hysterium pulchellum* Fries, Systema Mycologicum, vol. 2, p. 589. 1823.
Lophodermium melaleucum de Notaris, Giorn. Bot. Ital. 2 : 40. 1847.
Lophodermium melaleucum var. *aureo-marginatum* Stärback, Bot. Not. 1899. p. 159.
Lophodermium melaleucum var. *epiphyllum* Zeller, Mycologia 24 : 293. 1934.
Lophodermina melaleuca von Höhnel, Ber. der Deutsch. Bot. Gesellsch. 35 : 422.
   1917, and Ann. Mycol. 15 : 312. 1917.

Hysterothecia dull black, chiefly hypophyllous, in stramineous spots or scattered over the entire leaf, broadly elliptical with rounded ends, well arched, 400–950 μ long, 270–400 μ wide, up to 165 μ deep, subcuticular. Labia prominent and extroverted in age, heavily carbonized, 25–35 μ wide, lined inwardly by a bright orange mass of clavately expanded, nonseptate, gelatinously agglutinated and persistent periphyses up to 35 μ long and 1.5–2 μ wide. Basal layer a brown, translucent plate one to several cells thick, the bottom layer aliform and radiately disposed; this overlaid to a depth of 5–10 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover an aliform plate extending 10–15 μ beyond the basal layer at the margins, underlaid by brown, translucent pseudocollenchyma to a depth of 12–20 μ. Paraphyses hyaline, filamentous, straight or flexuous, clavately expanded

at the tips and gelatinously agglutinated to form a compact orange epithecium up to 10 μ thick, 80–90 μ long, 1–1.5 μ wide. Asci cylindrical to subclavate, asymmetrically subacute at the tips, tapered from about the middle to a short stipe, 65–80 μ long, 8–10 μ wide, 8-spored. Ascospores filiform, hyaline, nonseptate, of uniform diameter, straight or slightly twisted with the ascus, fasciculate and arranged in pairs, 50–60 μ long, 1.5–2 μ wide, incased in an inconspicuous, hyaline, gelatinous matrix. Mycelium of two kinds, one subcuticular, coarse, brown, 3–3.5 μ wide, distantly septate, and forming short aliform branches; the other very fine, hyaline, internal, 1–1.5 μ wide, aggregating into a close weft about the base of the hysterothecium.

Imperfect stage: According to von Höhnel (1918) *Sphaeria leptidea* Fries (K. vet Akad. Handl. 38 : 269. 1817 and Systema Mycologicum, vol. 2, p. 522. 1823) is not the perfect stage of this species. According to W. B. Grove (1922), *Leptothyrium melaleucum* Grove (Journ. Bot. 60 : 81. 1922) is associated with this species as an imperfect form in Perthshire, England. Grove reports, however, that *Lophodermium cladophilum* was on the stem parts of the same twigs and expresses the opinion that *L. melaleuca* is probably only a leaf form. This leaves the association of the Imperfect form uncertain.

Type locality: Not given by Fries.

Type specimen: Fries, Scleromyceti Succiae exs. No. 29.

Host: Vaccinium sp. : New Jersey (Ellis & Everhart, 1892) ; *V. ovatum:* Oregon (Zeller, spec.) ; *V. Vitis-idaea:* England (Grove, 1922), France (Roumeguère, exs.) ; Germany (Krieger, exs., Fuckel, exs.) ; Italy (Traverso, 1903), Sweden (Fries, 1823), Switzerland (Jaap, 1907).

Exsiccati: Fuckel, Fungi rhen. No. 736; Krieger, Schadl. Pilze, without number, Sept. 1900; Mougeot and Nestler, Stirp. Crypt. No. 654; Roumeguère, Fungi. sel. Gall. exs. Nos. 269 and 454.

Specimen: S. M. Zeller, Waldport, Ore., October, 1929. No. 7568.

Illustrations: Fries, Observ. mycol. praecip. ad illustr. floram Suec., pt. 1, pl. 2, fig. 1. 1815; Hilitzer, Vědecké spisy vydáv. Československ. Akad. Zeměd. 3 : pl. 1, fig. 5. 1929.

Notes: The *Phacidium Vaccinii* in Roumeguère's Fungi sel. Gall. exs. is typical *Lophodermina melaleuca.*

The species β *Hysterium pulchellum* of Fries, distinguished by its greenish yellow labia, is only old material in which the periphyses have become very dry and condensed. The colored mass of periphyses has also given rise to the variety *aureo-marginatum* Starbäck.   .

15. *Lophodermina nitens* (Darker) n. comb.

Hysterium pinastri Schrader, Schrader. Journ. Bot. 2 : 69. 1799, in part.
Hysterium limitatum Wiebel, Primitiae Florae Werth., p. 329, 1799, in part.
Aporia obscura Duby, Mém. Soc. Phys. et Hist. Nat Genève 16 : 63. 1861, in part.
Depazea linearis Rostrup, Tidsskr. Skovbr. 6 : 260. 1883, in part.
Hysterium pinastri β minor Westendorp, Herbier Crypt. Belge No. 68, (1841?).

Hysterothecia shining black, on the outer faces of needles and occurring singly, in pairs, or in pairs with one or two smaller hysterothecia in colonies, each colony cut off from adjacent ones above or below by very distinct, black, stromatic lines along which the leaves readily break, these lines double and composed of heavily carbonized and much compacted hyphal cells the terminations of which are aliform, elliptical, 650–1100 μ long, 350–525 μ wide, 150–300 μ high, subcuticular. Labia heavily carbonized, 40–70 μ wide, becoming widely separated and exposing nearly the entire hymenium, lined inwardly by a white mass of gelatinizing and soon evanescent, hyaline, clavately expanded periphyses 7–20 μ long and 1–1.5 μ wide. Basal layer a brown, translucent plate one to two cells thick, composed of radiately disposed, meandering, aliform plectenchyma; this overlaid to a depth of 20–30 μ by a closely interwoven, hyaline plectenchyma of very fine hyphae, from which the hymenium arises. Cover carbonized in the region of the labia, elsewhere more or less translucent, composed of an outer plate of radiately disposed aliform mycelium, which extends to a distance of 35–50 μ beyond the margin of the base, and an inner layer, several cells thick, of pseudocollenchyma. Paraphyses hyaline, filamentous, simple, nonseptate, clavately expanded at the tips, 65–100 μ long, 1.5–2 μ wide, shorter than the asci and forming no epithecium. Asci cylindrical to subclavate, asymmetrically subacute at the tips, tapered from above the middle to a broad stipe, 65–130 μ long, chiefly 11–13 but rarely up to 16 μ wide, 8-spored. Ascospores hyaline, nonseptate, filiform, fasciculate and arranged in pairs, straight or intricately coiled within the ascus, 60–120 μ long, 2–3.5 μ wide, incased in a conspicuous, hyaline, gelatinous matrix 2–3 μ thick.

Imperfect stage: Not named. Darker (1932) reports an Imperfect form with numerous, black, wrinkled or smooth, subcircular pycnidia 50 × 80 μ to 350–400 μ, subcuticular and applanate in section, 30–40 μ deep, with conidiophores 5–9 μ long and 2–4 μ thick seated upon a basal plectenchyma 7–12 μ thick, and cylindrical, bacillar conidiospores 6.5–10 μ long by 0.8–1.5 μ wide.

Type locality: Timagami, Ontario, Canada.

Type specimen: J. H. Faull, No. 4882, May, 1924, on *Pinus Strobus.*

Hosts: *Pinus* sp. (2-needle) : Italy (Anzi, exs.) ; *P. albicaulis:* California, Idaho, Oregon (Darker, 1932), Germany (Jaap, 1905) ; *P.*

Cembra: (Rehm, 1887), Austria (Jaap, 1908), France (Roumeguère, exs.) ; *P. montana:* Austria (Jaap, 1908), Germany (Jaap, 1905) ; *P. Lambertiana:* California (Boyce, spec.), Oregon (Darker, 1932) ; *P. monticola:* California, Idaho (Weir, spec.), Oregon, Washington (Darker, 1932) ; *P. radiata:* California (Wagner, spec.; Boyce, spec.) ; *P. halpensis:* Austria (Jaap, 1916), France (Roumeguère, exs.) ; *P. Strobus:* Massachusetts, Michigan, New Hampshire, Pennsylvania (Overholts, spec.), Washington (Boyce, spec.), Nova Scotia, Ontario (Darker, 1932), Saxony (Krieger, exs.), Germany (Rehm, 1887; Kunze, exs.) ; *P. rigida:* New Jersey (Ellis & Everhart, exs.) ; *P. ponderosa:* Pennsylvania (Overholts, spec.) ; *P. virginiana:* Pennsylvania (Orton and Hass, spec.).

Exsiccati: Anzi, Erb. Critt. Ital. II, No. 541; Bartholomew, Fungi Columb. No. 4426; Ellis & Everhart, Fungi Columb. No. 1029; Kunze, Fungi sel. exs. No. 371; Krieger, Fungi saxonici No. 2373; Krypt. exsic. ed. u Museo Palat. Vindob. No. 1611; Rabenhorst, Fungi europ. No. 461; Roumeguère, Fungi sel. Gall. exs. No. 456; Seymour & Earle, Economic fungi, No. 200; de Thuemen, Fungi austriaci No. 871; Reliquiae Farlowiana No. 50.

Specimens: W. W. Wagner, Monterey, Cal., Mar. 17, 1930; J. S. Boyce, San Francisco, Cal., Jan. 27, 1920; Hyampton, Cal., June 12, 1914; Silverton, Wash., May 22, 1916; Overholts, Greenwood Furnace, Pa., Oct. 18, 1919; L. O. Overholts, Millheim, Pa., Apr. 19, 1925; Orton and Hass, Pine Grove Mills, Pa., May, 1914; L. O. Overholts, Charter Oak, Pa., June 14, 1920; Weir, Priest River, Idaho, Aug. 3, 1915.

Illustrations: Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : pl. 20, figs. 10–15; pl. 27, fig. 2. 1932.

16. *Lophodermina orbicularis* (Ehrenberg) n. comb.

Hysterium orbiculare Ehrenberg, Fungos a viro clariss. Adalberto de Chamisso sub auspic. Romanzoff. in itinere circa terr. glob. coll. enum. novosque descrip. et pinxit, No. 30, 1820.
Lophodermium orbiculare Saccardo, Sylloge Fungorum 2 : 799. 1883.
Lophodermium orbiculare Ellis and Everhart, North American Pyrenomycetes, p. 717. 1892.
Hysterium gracile Ehrenberg, Fungos a viro clariss. Adalberto de Chamisso sub auspic. Romanzoff. in itinere circa terr. glob. coll. enum. novosque descrip. et pinxit, No. 31, 1820.
Lophodermium gracile Saccardo, Sylloge Fungorum 2 : 799. 1883.

Hysterothecia dark brown to black, shining, hypophyllous, in circular, light tan to cinereous, unlimited spots 2–4 mm. in diameter and these when situated near each other imbedded in wider dark brown dead areas, broadly elliptical, not greatly arched, with rounded ends, 375–525 μ long, 315–450 μ wide, subcuticular. Labia heavily carbonized, tending to become extroverted, nearly as long as the hysterothecium, 30–50 μ wide,

lined inwardly by a golden or orange mass of gelatinous, clavately expanded, persistent periphyses up to 25 μ long, 2.5–3 μ wide. Basal layer a brown, translucent plate of radiately disposed aliform hyphae; this overlaid to a depth of 5–7 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover rather flat, carbonized in the region of the labia, elsewhere more or less translucent, consisting of an outer plate of radiately disposed aliform cells underlaid to variable thicknesses by pseudocollenchymatous cells. Paraphyses hyaline, filamentous, straight or flexuous, not clavately expanded at the tips but bent or crushed and gelatinously agglutinated into a dense, tough, orange-yellow epithecium about 20 μ thick, 80–100 μ long, 1–1.5 μ wide. Asci cylindrical to subclavate, asymmetrically subacute or rounded at the tips, tapered from somewhat above the middle to a broad stipe, 55–80 μ long, 9–12 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, twisted within the ascus but not coiled, 35–55 μ long, 2–2.5 μ wide, incased in an inconspicuous gelatinous matrix.

Imperfect form: Unknown.

Type locality: Unalaska.

Type specimen: Not specified.

Hosts: *Andromeda axillaris:* North Carolina (von Schweinitz, 1834) ; *A. lycopodioides:* Unalaska (Ehrenberg, 1820) ; *Chamaedaphne calyculata:* New Hampshire (Farlow, exs.), Ontario (Ellis and Everhart, 1892; Rehm, 1911; Dearness, spec.; Jackson, spec.).

Exsiccati: Ellis & Everhart, North Amer. Fungi. No. 2376; Ellis & Everhart, Fungi Columb. No. 127: Reliquiae Farlowianae No. 49; Rehm, Ascomyceten, No. 1926.

Specimens: John Dearness, London, Ont., Aug. 30, 1890; H. S. Jackson, Bear Island, Lake Temagami, Ont., Aug. 21, 1930.

17. *Lophodermina Paeoniae* (Rehm) n. comb.

Lophodermium Paeoniae Rehm, in litt., according to Vestergren, Botan. Notis. 1897, p. 259.

Hysterothecia dull to shining black, abundant, usually crowded and often confluent end to end or laterally in extensive, stramineous, unlimited areas on stems, subrotund to narrowly elliptical, 300–350 μ wide, 400–700 μ long, subcuticular. Labia prominent, heavily carbonized, 25–30 μ thick, 20–40 μ wide, nearly as long as the hysterothecium, lined inwardly by a white mass of gelatinous, clavately expanded, much compacted, hyaline periphyses 5–12 μ long by 1 μ wide. Basal layer a brown, translucent plate of loosely compacted, radially disposed aliform mycelium thickened, especially toward the center, by the apposition, above, of 2–5 layers of

brown, pseudoparenchymatous cells, this overlaid to a depth of 5–15 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover carbonized in the region of the labia, elsewhere more or less translucent, composed of an outer plate of brown, heavily chytinized, radially disposed aliform mycelium which extends outward 20–30 μ beyond the margin of the base and is thickened by the apposition, beneath, of 1–3 layers of brown, pseudocollenchymatous cells. Paraphyses hyaline, filamentous, straight or flexuous, nonseptate, simple, not clavately expanded but bent or crushed by pressure and gelatinously coalesced into a thin, white epithecium, 40–80 μ long, 1–1.5 μ wide. Asci cylindrical to subclavate, asymmetrically and bluntly rounded above, tapered from above the middle to a fine stipe up to 10 μ long, 65–80 μ long, 6–8 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 55–65 μ long, 1–1.5 μ wide, incased in an inconspicuous gelatinous matrix about 1 μ thick.

Imperfect stage: Unknown.

Type locality: Gotlandia, according to Vestergren (1897).

Type specimen: Not designated.

Hosts: *Paeonia* sp. : (Vestergren, 1897) ; *P. sinensis:* Germany, (Sydow, exs.).

Exsiccati: Sydow, Mycoth. Germ. No. 2534.

18. *Lophodermina prunicola* n. sp.

Hysterothecia small, shining black, scattered in light brown, extensive areas on the upper faces of leaves and on the petiole and the mid-vein beneath, broadly elliptical with somewhat pointed ends, 450–685 μ long, 270–435 μ wide, well arched above; subcuticular. Labia narrow and heavily carbonized, 25–35 μ wide, 20–25 μ thick, lined along the inner edges with a mass of white, clavate, gelatinously compacted and soon evanescent periphyses 2–2.5 μ wide and 10–15 μ long. Basal layer a plate one cell thick of radiately disposed, brown, translucent, aliform mycelium, this overlaid to a depth of 8–12 μ by a closely interwoven, hyaline layer of fine plectenchyma. Cover well arched, not heavily carbonized, translucent except in the lip region, of aliform construction throughout the top and radiately aliform at the margins, with a heavy deposit of pseudocollenchymatic cells toward the center, up to 20 μ thick. Paraphyses hyaline, filamentous, straight or flexuous, bent or crushed at the tips in the center of the hymenium, uncinate toward the margins, not swollen or gelatinously agglutinated, hardly exceeding the asci, 50–70 × 1–1.5 μ. Asci cylindric to subclavate, asymmetrically subacute at the tips, tapered from near the top to a short but fine stipe, 45–70 μ long, 6–8 μ wide,

8-spored.   Ascospores hyaline, filamentous, straight or slightly twisted within the ascus, fasciculate and arranged in pairs, blunt at both ends and of uniform diameter throughout their length, 35–60 × 0.75–1 μ, gelatinous matrix hyaline, inconspicuous.

Imperfect stage: Unknown.

Type locality: Ouray, Colorado.

Type specimen: Clements' Cryptogamae Formationum Coloradensium No. 465.

Host: *Prunus demissa:* Colorado (Clements, exs.).

Notes: This material was identified and distributed by Clements under the name *Lophodermium hysteroides* (Pers.) Sacc., which it resembles in some respects.   It is, however, the first record of a fungus of this type on Prunus and differs from *Lophodermellina hysteroides,* which is known to occur on other members of the Rosaceae, in being subcuticular as well as in the size of its hysterothecia, asci, and spores.

19. *Lophodermina punctiformis* (Fries) n. comb.

Hysterium petiolare de Albertini and von Schweinitz, Conspect. fung. in Lusat. superior. agro Niski, cresc., p. 59. 1805.
Hysterium punctiforme Fries, Observ. mycol. pracip. ad illustr. floram Suec., pt. 2, p. 356. 1818; K. Vet. Akad. Handl. 40 : 103. 1819; Systema Mycologicum, vol. 2, p. 593. 1823.
Lophodermium petiolare Chevallier, Flore gén. des env. de Paris, vol. 1, p. 436. 1826.
Lophodermium petiolicolum Fuckel, Jahrb. d. Nassauischen Ver. f. Naturk. 23/24 : 255. 1869.
Lophodermium punctiforme Fuckel, Jahrb. d. Nassauischen Ver. f. Naturk. 23/24 : 255. 1869.
Hysterium punctiforme Oudeman, Nederl. Kruidk. Arch., ser. 2. 1 : 50. 1872.
Lophodermium echinophilum Spegazzini, according to Saccardo, Michelia 1 : 56. 1877.

Hysterothecia shining black, scattered in stramineous areas on petioles, large nerves and leaf blades, on small nerves oriented parallel with the nerve axis, on petioles and blades without orientation, elliptical to nearly linear, acutely rounded at the ends, amphigenous, straight or unequilateral and lunate, 650–1500 μ long, 340–400 μ wide, subcuticular. Basal layer a light brown, translucent plate one cell thick, consisting of radiately disposed aliform hyphae emanating from an elongated, narrow, central pseudoparenchyma; this overlaid to a depth of 10–15 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises.   Labia well defined, heavily carbonized, 50–65 μ wide, reaching to within 175 μ of each end of the hysterothecium, lined inwardly by a densely agglutinated, white mass of evanescent periphyses up to 20 μ long, 2.5–3 μ wide.   Cover heavily carbonized at the margins and in the labia, in the intervening area more or less translucent, con-

sisting of an outer plate of radiately disposed, aliform, meandering prosenchyma thickened by the apposition, beneath, of 2 to 4 rows of pseudocollenchymatous cells.   Paraphyses hyaline, filamentous, straight or flexuous, not clavately expanded but crushed and bent at the tips by pressure, 60–90 μ long, 1–1.5 μ wide, gelatinously agglutinated above the asci into a white epithecium 5–10 μ thick.   Asci cylindrical to sub-clavate, asymmetrically subacute at the tips, tapered below to a long thin stipe, 45–77 μ long, 5.5–6.5 μ wide, 8-spored.   Ascospores hyaline, fili-form, nonseptate, fasciculate and arranged in pairs, straight or slightly twisted with the ascus, 33–50 μ long, 1–1.5 μ wide, incased in a hyaline, gelatinous matrix 1.5–2 μ thick.

Imperfect stage: Leptostroma petiolicolum Hilitzer, Vĕdecké spisy vydáv. Českoslov. Akad. Zemĕd. 3 : 88. 1929.–Pycnidia intermixed with the hysterothecia, shining black, subcuticular, round, 100–300 μ in diameter, up to 75 μ high, wall consisting of meandering, aliform prosen-chyma, brown above, nearly hyaline below.   Conidiophores hyaline, taper-ing from 2 μ wide at the base to 1 μ at the tips, septate, unbranched. Conidia bacilliform, hyaline, nonseptate, 4–5 μ long, 1 μ wide.

Type locality: Not given by Fries.

Type specimen: Not given by Fries.

Hosts: *Castanea sativa:* (Rehm, 1887; Saccardo, 1877), Austria (Jaap, 1916), Czechoslovakia (Hilitzer, 1929) ; *Quercus* sp. : Germany (Rehm, 1887), France (de Thuemen, exs.) ; Russia (Potebnia, 1910) ; *Q. lanuginosa:* Austria (Jaap, 1916) ; *Q. Robor:* Saxony (Rabenhorst, exs.) ; *Q. rubra:* France (Roumeguère, exs.), Germany (Sydow, exs.), Czechoslovakia (Hilitzer, 1929) ; *Q. sessiliflora:* Czechoslovakia (Hil-itzer, 1929) ; *Fraxinus* (Rehm, 1887; Roumeguère, exs.) ; *Acer* (Fries, 1823) ; *A. saccharinum:* New York (Ellis & Everhart, 1892).

Exsiccati: Rabenhorst, Fungi europ. Nos. 462, 2642; Roumeguère, Fungi sel. exs. No. 7044; Roumeguère, Fungi Gallici exs. Nos. 1659, 1660; Sydow, Mycoth. Germ. No. 1345; de Thuemen, Mycoth. univ. No. 1757.

Note: *Hysterium petiolare* as illustrated in Desmazière's exsiccati Ser. 2, Nos. 181 and 563 is, according to Duby (1861, p. 64), Peziza.   I have not seen these specimens.

20. *Lophodermina Rhododendri* (von Schweinitz) n. comb.

Plate III, Fig. 12.

Hysterium Rhodendri von Schweinitz, Trans. Am. Philos. Soc., n.s. 4 : No. 2116. 1834.

Hysterium sphaerioides var. *Rhododendri* Rabenhorst, Fungi europaei No. 355. 1861.

?*Lophodermium Rhododendri* de Cesati, Rendic. Acc. Sci. fisich. e matem. di
   Napoli 9 : No. 537. 1870.
Coccomyces Rhododendri Saccardo, Sylloge Fungorum 8 : 748. 1889.
Lophodermium Rhododendri Ellis and Everhart, North American Pyrenomycetes,
   p. 717. 1892.

Hysterothecia dull black, amphigenous, scattered in light stramineous,
irregular spots 2–10 mm. or more in diameter and conspicuously limited
by a black, stromatic line, oval, ends tapered and rounded, 750–1350 μ
long, 340–675 μ wide, subcuticular. Labia conspicuous, well arched,
carbonized, 20–50 μ wide, up to 35 μ thick, lined inwardly by a white
mass of gelatinous, soon evanescent hyaline, clavately expanded, septate
periphyses 10–15 μ long and 5–7 μ wide. Basal layer a brown, translu-
cent plate one or two cells thick consisting of radiately disposed, definitely
aliform prosenchyma; this overlaid to a depth of 10–15 μ by a closely
interwoven and compacted hyaline plectenchyma of very fine hyphae
from which the hymenium arises. Cover well arched, carbonized in the
region of the labia, somewhat carbonized near the margins, but in the
intervening area more or less translucent, the outer, aliform plate ap-
pearing distinctly netted because of the blackening of the epidermal cell
walls. Paraphyses hyaline, filamentous, guttulate, straight and slightly
clavately enlarged at the tips, 100–125 μ long, not exceeding the asci
and not uniting into an epithecium. Asci cylindrical to subclavate,
asymmetrically rounded to subacute at the tips, tapered toward the
base to a short, moderately fine stipe, 80–125 μ long, 9–14 μ wide,
8-spored. Ascospores filiform, hyaline, of uniform diameter, fasciculate
and arranged in pairs, 66–90 × 2–2.5 μ wide, inclosed in a conspicuous
hyaline, gelatinous matrix up to 2 μ thick.

Imperfect stage: Unknown.

Type locality: Bethlehem, Pennsylvania.

Type specimen: von Schweinitz, Bethlehem, Pa., on Rhododendron.

Hosts: *Rhododendron:* Pennsylvania (von Schweinitz, 1834; Orton,
spec.; Overholts, spec.; Overholts and Kirby, spec.); Oregon (Zeller,
spec.); *R. californicum:* Oregon (Zeller, spec., 1927), New York (Ellis
& Everhart, 1892); *R. catawbiense:* North Carolina (Ellis & Everhart,
1892) Tennessee (Charles, spec.); *R. ferrugineum:* Central Alps (Rehm,
1887); *R. maximum:* Pennsylvania (Overholts, spec.), West Virginia
(Ellis, exs.).

Specimens: C. R. Orton, Galbraith's Gap, Center Co., Pa., Apr. 30,
1918; L. O. Overholts, Cooke Forest, Cooksburg, Pa., Aug. 16, 1927
and Aug. 17, 1927; Bear Meadows, Pa., Aug. 11, 1921 and May 13,
1925; Ingleby, Center Co., Pa., July 13, 1929; Stone Creek, Hunt Co.,
Pa., Aug. 6, 1927; Coxe's Valley, Mifflin Co., Pa., June 9, 1921; Stone
Valley, Huntingdon Co., Pa., Jan. 2, 1921; L. O. Overholts and R. S.

Kirby, Stone Valley, Pa., Aug. 10, 1924; Vera K. Charles, Roan Mountain, Tenn., 1909; S. M. Zeller, Alsea Mt., Ore., June 17, 1922, No. 2340, and June, 1922, No. 2359.

Exsiccati: Ellis, North Amer. fungi No. 1287; Ellis & Everhart, Fungi Columb. No. 738; Rabenhorst, Fungi europ. Nos. 355, 458; Rehm, Ascomyceten No. 126.

21. *Lophodermina septata* n. sp.

Hysterothecia shining black, amphigenous, solitary in light stramineous areas sharply delimited by black, stromatic lines from uninfected distal and proximal parts, broadly oval with rounded to truncate ends, subcuticular, 800–1200 μ long, 400–625 μ wide. Labia indistinct, not at all or only very slightly carbonized, neither arched nor extrovert in age, 8–20 μ wide, lined inwardly by a white mass of hyaline, clavately enlarged, gelatinously agglutinated, persistent periphyses 10–25 μ long and 2.5–3 μ wide. Cover somewhat arched, thin and not carbonized, consisting of heavily chytinized, translucent, light brown, meandering aliform mycelium, somewhat thickened in the region of the labia by the deposition of one to several layers of translucent pseudocollenchyma. Basal layer a plate one cell thick of brown, translucent, radiately disposed, aliform mycelium, sometimes thickened near the center by deposition on the upper side of one or two layers of pseudoparenchyma; this overlaid to a depth of 10–25 μ by a very closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Paraphyses hyaline, filamentous, nonseptate, straight or flexuous, not clavately expanded above, shorter than the asci and not forming an epithecium. Asci long cylindric to clavate-cylindric, asymmetrically long-acute at the tips, tapered from near the apex to a fine, long stipe, 115–165 μ long, 10–14 μ wide, 8-spored. Ascospores hyaline, fasciculate and arranged in pairs, clavate-filiform, 85–120 μ long, 1.5–2 μ wide at the tips, tapered to less than 1 μ wide at the base, straight or coiled within the ascus, incased in a conspicuous, hyaline, gelatinous matrix 2–3 μ thick, the spores septate at intervals of 8–15 μ.

Type locality: Knappa, Clatsop County, Oregon.
Type specimen: E. J. Perkins, May 3, 1919. No. K-1000.
Host: *Picea sitchensis:* type locality only.

22. *Lophodermina Thuyae* (Davis) n. comb.
Plate II, Fig. 7.
Lophodermium Thuyae Davis, Trans. Wisc. Acad. Sci., Arts and Lett. 20 : 424. 1922.

Hysterothecia shining black, amphigenous on dead needles, elliptical, with abruptly rounded ends, 525–950 μ long, 225–500 μ wide, subcuticular.

Labia prominent and well arched and spreading, heavily carbonized in the central parts, less so or not at all toward the ends, up to 80 μ wide and 45 μ thick in the middle, tapering to lesser widths toward the ends, lined inwardly with a white mass of clavately enlarged, gelatinously agglutinated and soon deliquescent, hyaline periphyses 7–15 μ long and 1–1.5 μ wide. Basal layer a brown, translucent plate one cell thick, consisting of radiately disposed, digitate, aliform prosenchyma; this overlaid to a depth of 20–30 μ by a closely interwoven, hyaline plectenchyma of fine hyphae with an upper columnar layer 10–15 μ thick, from which the hymenium arises. Cover well arched, translucent except in the region of the labia, consisting of an outer plate of digitately branched aliform hyphae and a considerable deposit, on the lower side, of pseudocollenchymatous cells. Paraphyses hyaline, straight or flexuous, simple, clavately enlarged at the tips, often also much bent or crushed by pressure, coalescing in a gelatinous, white epithecium 5–10 μ thick, 100–130 μ long, about 2 μ wide. Asci quite regularly cylindrical, asymmetrically acute at the tips, abruptly narrowed at the base to a very short stipe and broad foot, 95–125 μ long, 8–12 μ wide, regularly and without exception 4-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, rounded at the tips and tapered to a subacute base, 80–115 μ long, 1.5–2 μ wide, incased in a conspicuous, hyaline, gelatinous matrix 2–2.5 μ wide.

Imperfect stage: Unknown.

Type locality: Saxon, Wisconsin.

Type specimen: Davis, Fungi Wisconsinenses exsiccati No. 114.

Host: *Thuja occidentalis:* New Hampshire (Darker, 1932), Wisconsin (Davis, 1922 and exs.), Ontario (Darker, 1932).

Exsiccati: Davis, Fungi. Wisc. exs. No. 114.

Illustrations: Davis, Trans. Wisc. Acad. Sci., Arts and Lett. 20 : 425, fig. 2, 1922: Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : pl. 21, figs. 6–9. 1932.

23. *Lophodermina uncinata* (Darker) n. comb.

Lophodermium uncinatum Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : 76. 1932.

Hysterothecia shining brownish black, amphigenous but chiefly epiphyllous, scattered, usually discrete but occasionally becoming confluent end-to-end, narrowly elliptical to rectangular and bluntly rounded to truncate at the ends, 500–2250 μ long, 200–500 μ wide, 190–300 μ deep, subcuticular. Labia heavily carbonized but indistinct and merging into the cover, lined inwardly by a white mass of clavately expanded, gelatinizing and soon evanescent periphyses 8–20 μ long and 1–1.5 μ wide.

Basal layer a brown, translucent plate one or two cells thick, composed of radiately disposed, aliform prosenchyma; this overlaid to a depth of 15–30 μ by a closely interwoven, hyaline plectenchyma of fine hyphae from which the hymenium arises. Cover carbonized at the margins and in the regions of the labia, the intervening area more or less translucent, composed of an outer aliform plate, which extends to a distance of 15–70 μ beyond the margin of the basal layer, thickened by the apposition, beneath, of pseudocollenchymatous cells to a depth of 40–60 μ. Paraphyses hyaline, filamentous, simple, nonseptate, not clavately expanded at the tips but often strongly uncinate, exceeding the asci and gelatinously agglutinated into a white epithecium up to 25 μ thick. Asci cylindrical to subclavate, asymmetrically subacute at the tips, tapered from about the middle to a fine stipe, 100–135 μ long, 12–15 μ wide, 8-spored. Ascospores hyaline, filiform, nonseptate, fasciculate and arranged in pairs, straight or somewhat twisted with the ascus, 50–75 μ long, 1.5–2 μ wide, incased in a conspicuous, hyaline, gelatinous matrix 3–4 μ thick.

Imperfect form: Not named: Darker (1932) reports an associated imperfect form with pycnidia which form small, rounded or elliptical blisters, yellowish to reddish orange at first and black at maturity, subcuticular in position, 160–325 μ long, 110–210 μ wide, with hyaline, bacillar, conidia 4–6 μ long and 0.8–1 μ wide. The hyphae making up these pycnidia have the same aliform characters as is evident in the hysterothecia.

Type locality: Government Camp, Clackamas County, Oregon.

Type Specimen: G. D. Darker, July, 1929, on *Abies amabilis*, No. 275 in the Arnold Arboretum Pathological Herbarium.

Host: *Abies amabilis: Oregon* (Darker, 1932), Washington (Grant, spec.).

Specimens examined: Darker's type specimen; Herb. J. M. Grant, *"Lophodermium Abietis,"* Marysville, Wash., March, 1927.

Illustrations: Darker, Contrib. Arnold Arboretum of Harvard Univ. 1 : pl. 20, fig. 16. 1932.

24. *Lophodermina versicolor* (Wahlenberg *ex.* Fries) n. comb.

Hysterium versicolor Wahlenberg, Flora Lapponica, p. 522, 1812.
Hysterium versicolor Fries, Systema Mycologicum vol. 2, p. 592, 1823.
Lophodermium versicolor Rehm, in Rabenhorst's Kryptogamen Flora, vol. 3, p. 48. 1887.

Hysterothecia small, shining black, amphigenous in light, yellowish spots of very variable size on the blades of dead leaves, subcuticular, 350–600 μ long, 150–375 μ wide, broadly elliptical with bluntly rounded ends. Labia only lightly carbonized, extroverted, as long or nearly as

long as the hysterothecium, up to 85 μ wide in the central portion and tapered to as little as 10 μ wide at the ends, lined inwardly with a persistent yellow mass of nongelatinized, clavately expanded, periphyses 15–25 μ long and 1.5–2 μ wide. Basal layer a plate one cell thick of brown, translucent, radiately arranged aliform hyphae, this overlaid to a depth of 12–20 μ by a yellow, intricately interwoven, fine plectenchyma. Cover a thin, non-carbonized plate of meandering aliform hyphae overreaching the basal layer at the margins and there forming a rim or skirt of aliform cells, the central portions underlaid by a thin development of pseudo-collenchymatous cells. Paraphyses straight or variously curved, much bent and crushed above by pressure, and intertwining above the asci to form a thin yellow epithecium, 60–85 μ long, 1–1.5 μ thick, without gelatinous coating. Asci cylindrical to subclavate, asymmetrically and conically subacute at the tips or bluntly and asymmetrically rounded, tapered from above the middle, 35–75 μ long, 5–8 μ wide, 8-spored. Ascospores hyaline to yellow-tinted, straight in the longest asci, in the others often intricately coiled, fasciculate and arranged in pairs, 25–45 μ long, 0.75–1 μ wide, without evident gelatinous matrix:

Imperfect stage: Unknown.

Type locality: Not specified.

Type specimen: Not specified.

Hosts: *Salix hastata* (Fries, 1823); *S. arbuscula* (Fries, 1823); *S. herbacea* (Lind, 1905); *S. glauca* (Lind, 1905); *S. retusa:* Germany (Rehm, 1896); *S. pentandra:* Pennsylvania (Overholts, spec.); *S. pseudolapponum:* Colorado (*Clements, exs.*).

Exsiccati: Clements, Crypt. Format. Colo. No. 49.

Specimen: L. O. Overholts, Greenwood Furnace, Pa., May 15, 1925.

Illustrations: Wahlenberg, Flora Lapp. pl. 30, fig. 5. 1812.

Notes: Rehm (1896) gives no details of the asci and spores in his description of this species and lists it among the doubtful. According to Lind (1905), it should be regarded as the same as *L. hysterioides,* as should also the report by Rostrup (Bot. Tidsskr. 25 : 310. 1903) of *L. maculare* on *Salix glauca.* The writer has not seen any material from Europe; but the material in Clements' Cryptogamae Formationum Coloradensium No. 49 has furnished good asci, spores and paraphyses. Wahlenberg's comment that this is a beautiful species is justified by the yellow mass of persistent periphyses, which fringe the extroverted labia, and the bright yellow epithecium.

EXCLUDED SPECIES

Among the 131 recorded species names directly assigned at one time or another to Lophodermium it is natural that, besides those that are syn-

onyms, certain names will have been used to designate fungi not properly capable of being included within Lophodermium or the three derivatives of it discussed in this paper. The following list indicates these incompatible species and gives the treatments that have been accorded them.

1. *Lophodermium Abietis-concoloris* Mayr

Die Waldungen von Nordamerika, p. 336. 1890.

According to Dearness (1924), the material upon which this name was based was too immature to describe. The species is figured by von Tubeuf (1901, p. 16), and Dearness (*l. c.*) has concluded that it is the same as material studied by him, which had been taken by J. S. Boyce (No. 732) in Baker County, Oregon, and by E. Bethel in Colorado on *Abies concolor.* Dearness has renamed the species *Hypodermella Abietis-concoloris* (Mycologia 16 : 150. 1924).

2. *Lophodermium amplum* Davis

Trans. Wisconsin Acad. Sci., Arts and Lett. 19 : 695. 1919.

This species was described on *Pinus Banksiana* from Wisconsin and Dearness (1924) reports it also on *Pinus contorta* from Oregon. Dearness (*l. c.*) finds it closely similar to *Hypodermella sulcigena* on *Pinus sylvestris* but maintains it as a separate species under the name *Hypodermella ampla* Dearness (Mycologia 16 : 152. 1924).

3. *Lophodermium brachysporum* Rostrup

Tidsskr. Skovbr. 6 : 281. 1883.

Von Tubeuf (1895, p. 247) transferred this species to Hypoderma; and Darker (1932, p. 25) considered it as synonymous with *Hypoderma Desmazierii* Duby.

4. *Lophodermium gilvum* Rostrup

Tidsskr. Skovbr. 6 : 283. 1883.

It has been shown by Darker (1932, p. 92) that this name is synonymous with *Naemacyclus niveus* (Pers. *ex* Fries) Saccardo.

5. *Lophodermium infectans* Mayr

Die Waldungen von Nordamerika, p. 336. 1890.

Boyce (1927) has shown that this is synonymous with *Hypoderma robustum* von Tubeuf.

6. *Lophodermium lineare* Ellis and Everhart

The North American Pyrenomycetes, p. 721. 1892.

This fungus is remarkable in that it is without paraphyses and has ascospores 5-8 μ wide at the ends but distinctly narrower in the middle. It has been made by von Höhnel (1917) the type species of his genus Bifusella and has as synonyms *Hypodermium effusum* von Schweinitz, *Rhytisma lineare* Peck, and *Hypoderma lineare* de Thuemen.

7. *Lophodermium lineatum* Smith and Ramsbottom

Trans. Brit. Mycol. Soc. 6 : 365. 1920.

The description of the species is based on material taken from *Pinus excelsa* at Wexford, Ireland. The asci range from 70 to 105 μ in length by 18–20 μ wide. The ascospores are 25–35 μ long by 2.5–3 μ wide. Darker (1932) is right in regarding this as a synonym of *Hypoderma Desmazierii* Duby.

8. *Lophodermium nervisequium* Chevallier

Flore général des environs de Paris, vol. 1, p. 435. 1826.

This is one of the species originally transferred from Hysterium by Chevallier when he established the genus Lophodermium. Its synonyms are *Hypoderma nervisequium* De Candole (1815), *Lophoderma nervisequium* Chevallier (1822), *Hysterium nervisequium* Fries (1823), *Hypodermium nervisequium* Link (1825), *Schizoderma nervisequium* Duby (1830), and *Daedalea nervicola* Hazslinsky (1887).

Lagerberg (1910, p. 148) transferred it to Hypodermella, because of its distinctly clavate spores; and Darker (1932) has found that it is not a homogeneous species and has separated from it a form with inconspicuous, colorless pycnidia to which he has given the name *Hypodermella lirelliformis* (Darker, *l. c.*, p. 45). It has also been transferred by von Höhnel (1916, p. 54) to his genus Hypodermina.

9. *Lophodermium Petersii* Saccardo

Sylloge Fungorum 2 : 795. 1883.

This is a North American fungus described by Berkeley and Curtis (1859) as *Hysterium Petersii* "*in Cupressi v. Juniperi* (Cedar) *foliis* (?). Alabama." It is not a Lophodermium but is properly identifiable as *Clithris Juniperi* (Karst.) Rehm.

10. *Lophodermium platyplacum* Saccardo

Sylloge Fungorum 2 : 792. 1883.

This fungus, on Clusia, was originally named *Hysterium platyplacum* by Berkeley and Curtis (1869, p. 792). I have not seen original material, and the transcription of the description by Saccardo (*l. c.*, 1883) is not sufficient for an accurate diagnosis. I have, however, examined a specimen, identified as this species, which was collected by Dr. Fred J. Seaver in the island of Trinidad. Seaver's material is not a Lophodermium. The hysterothecium lacks a definite ostiole and periphyses, and its base and cover are apparently continuous pseudocollenchyma. It is, however, identical with *Clithris Clusiae* Tehon (1918).

Assuming that the fungus described by Berkeley and Curtis from Cuba is identical with that described by Tehon from Porto Rico and that collected in Trinidad by Seaver, the proper name would be *Clithris platyplacum* (Berkeley and Curtis) n. comb.

This is in accord with the opinion of von Höhnel (1917, p. 311) who examined the type specimen (Fungi Cubensis Wrightiani No. 725) and described the fungus contained therein as an "überreife Phacidiaceae, deren Gattungs zugehörigkeit unsicher ist. Zwischen der Blattepidermis und den Palissadenzellen sind zwei Lagen von tafelformigen Parenchymzellen eingeschaltet, in deren ausserer Lage sich der Fruchtkörper entwickelt."

11. *Lophodermium Rubi* Chevallier

Flore général des environs de Paris, vol. 1, p. 436. 1826.

Persoon named this fungus *Hysterium virgultorum* in 1796 (p. 84); Chevallier (1822, p. 31) named it *Lophoderma Rubi*; and Fries called it *Hysterium Rubi* (1823, p. 587). But De Candole (1815, p. 165) placed it in his genus *Hypoderma* under the specific name *virgultorum*. Chevallier transferred it, with his other species, to Lophodermium in 1826. Since the revival of De Candole's genus Hypoderma by de Notaris (1847), this fungus has been quite properly known as *Hypoderma virgultorum* (Persoon) De Candole.

12. *Lophodermium javanicum* Penzig and Saccardo

Icones fungorum Javanicorum, p. 65. 1904.

It has been pointed out by von Höhnel (1917, p. 312) that in this species the intraepidermal ascoma is surrounded to a distance of 100 μ by epidermal cells filled with black, opaque material. This apparently is stromatic, and removes the species from Lophodermium. I have not

seen material of it; but its characters as published indicate a close relationship to Xyloma Pers., according to the analysis of von Höhnel (1917, p. 419).

13. *Lophodermium Sambuci* Rehm

Rabenhorst's Kryptogamen-Flora 3 : 48. 1887.

First named by Schumaker (1803, p. 152) *Hysterium Sambuci*, it was transferred to Lophodermium by Rehm (*l. c.*) with a query as to its possible relationship to the Lophiostomataceae. Rostrup (1885), however, had shown that Schumaker designated with his name the fungus to which Persoon applied the name *Opegrapha varia* in 1794. According to Lind (1905), the fungus on Sambucus is not a Lophodermium.

14. *Lophodermium Phacidium* de Notaris

Giorn. Bot. Ital. 2 : 42. 1847.

Rehm (1896, p. 1248) has made this a synonym of *Coccomyces coronatus* (Schum.) de Not.

15. *Lophodermium cladophilum* Rehm

Rabenhorst's Kryptogamen-Flora 3 : 42. 1887.

This species is redescribed and transferred to the genus Bifusella in the following section (p. 117).

16. *Lophodermium Lauri* Rehm

Rabenhorst's Kryptogamen-Flora 3 : 37. 1887.

Rehm's disposition of this fungus is called in question, since the ascospores are less than one-half the length of the ascus. Redescription is given in the following section (p. 120).

17. *Lophodermium Ameplodesmi* de Cesati, in literature

The Lophodermium on *Ampelodesmus tenax*, to which this name is applied in literature, is properly called *Lophodermium eximium* de Cesati (p. 48). *Hypoderma Ampelodesmi* de Cesati is another fungus on the same host and is characterized by having loculate hysterothecia and 2-celled ascospores (p. 122).

18. *Lophodermium scirpinum* (Persoon *ex* Fries) Chevallier

Hysterium scirpinum Persoon, in Mougeot and Nestler. Stirpes Cryptogamae
  Vogeso-Rhenanae quas in Rheni superioris inferiorisque, nec non Bogesorum
  praefecturis collegerunt. No. 475. 1815.
Hypoderma scirpinum DeCandolle, Flore française, 5 : 166. 1815.
Hysterium scirpinum Fries, K. Vet. Akad. Handl. 40 : 95. 1819.
Lophoderma scirpinum Chevallier, Journ. de Physique 94 : 31. 1822.
Hysterium scirpinum Fries, Systema mycologicum 2 : 590. 1823.
Lophodermium scirpinum Chevallier, Flore gén. d. env. d. Paris. 1 : 436. 1826.

I have had for examination material on *Scirpus lacustris,* the host
indicated by Fries (1823, p. 590), distributed in Roumeguère's Fungi
Sel. Gall. exs. No. 168. This material is definitely identifiable as a Hypo-
derma; and the proper designation for the species appears therefore
to be *Hypoderma scirpinum* (Persoon) DeCandolle.

REPLACEMENT OF SPECIES

IN THE EXAMINATION of specimens upon which the body of this paper
is based, it was found that four fungi encountered were not classifiable
in the categories given in the systematic and descriptive section. These
are given proper placement below.

1. *Bifusella Vaccinii* (Carmichael) n. comb.
Text–Fig. 1.

Hysterium Vaccinii Carmichael, in J. E. Smith's English Flora, vol. 5, pt. 2, p. 295.
  1836.
Hysterium cladophilum Leveille, in Mougeot and Nestler, Stirp. Crypt. No. 1243.
  1850.
Sporomega cladophila Duby, Mem. Soc. Phys. et Hist. Nat. Geneve 16 : 60. 1861.
Lophodermium cladophilum Rehm, in Rabenhorst's Kryptogamen-Flora 3 : 42.
  1887.
Lophodermium Vaccinii Schröter, Kryptogamenflora von Schlesien, vol. 2, p. 177.
  1908.

Hysterothecia appearing golden brown, scattered or crowded in dead
portions of stems, not in distinguishable spots, broadly ellipitical with
somewhat truncated ends, 450-675 μ long, 325-375 μ wide, subepidermal,
often oriented with the long axis at an angle to the axis of the stem, the
host epidermis splitting lengthwise of the stem regardless of the orienta-
tion of the hysterothecium. Labia indefinite, somewhat thickened and
carbonized in the middle, two-thirds to three-fourths the length of the
hysterothecium. Basal layer a thin plate of loose pseudoparenchyma
browned at the unions of cells but scarcely distinguishable from the thin,

hyaline plectenchyma from which the hymenium arises. Cover a compact, brown, more or less translucent plectenchyma underlaid to varying thicknesses by brown pseudoparenchyma. Paraphyses filamentous, hyaline, straight or flexuous, not clavately expanded but variously bent or crushed at the tips which are gelatinously fused into a thin, readily dissolved,
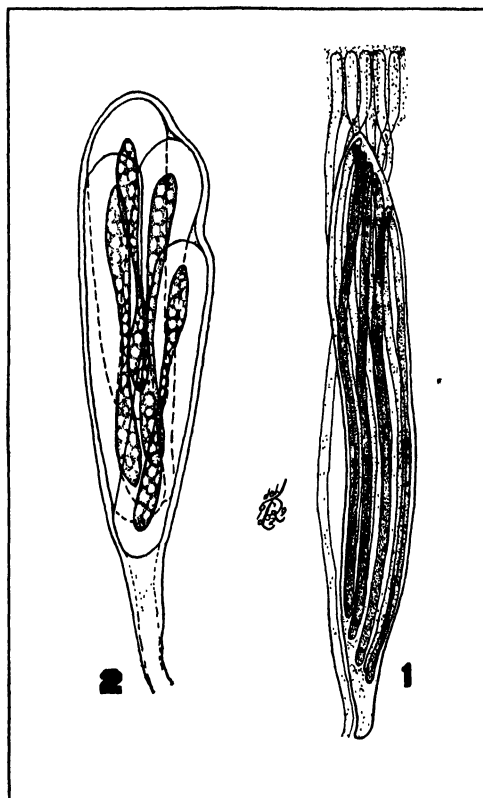
TEXT-Fig. 1.—Asci and spores of Dermascia and of Bifusella: (1) *Dermascia caricina*, ascus with spores and paraphyses (Roumeguère, Fungi sel. exs. No. 7142); (2) *Bifusella Vaccinii*, ascus showing the four bifusiform spores and the prominent gelatinous matrix of each spore (Reliquiae Farlowiana No. 46).

white epithecium, 90-115 μ long, about 1 μ wide. Asci clavate, truncately rounded above, tapered to a long, fine stipe, 85–100 μ long, 15–20 μ wide, 4-spored. Ascospores hyaline, nonseptate, bifusiform, 55–62 μ long, 4–5 μ wide, incased in a conspicuous, hyaline, cylindrical, gelatinous matrix 2.5–3 μ thick.

Imperfect stage: Unknown.

Type locality: Unknown.

Type specimen: ?Mougeot & Nestler, Stirp. Crypt. No. 1243.

Hosts: *Vaccinium Myrtillus:* England (Carmichael, *l. c.;* Cooke, 1871; Massee, 1895), Vosges Mountains (Jaap, 1911); *Vaccinium pennsylvanicum:* New Hampshire (Reliq. Farl.), New Jersey (Ellis and Everhart, 1892).

Exsiccati: Reliquiae Farlowiana No. 46. Rehm cites also Fuckel, Fungi rhen. No. 1967; Kunze, Fungi sel. No. 373; Rabenhorst, Herb. myc. II, No. 260; and de Thuemen, Fungi austr. No. 507.

Illustrations: Cooke, Handbook of British Fungi, p. 764, fig. 360. 1871.

Note: Bifusella, according to von Höhnel (1917, p. 418), is subcuticular and stromatic, neither of which characters the above fungus possesses. It is, however, the only genus distinguished by bifusiform spores; and it appears logical at present to include in it the above species.

2. EPIDERMELLA new genus

Genus of the Hypodermataceae with subrotund to linear ascomata developed beneath the cuticle and above the epidermis, opening by means of an elongated ostiole lined by gelatinizing, persistent or evanescent periphyses. The ascoma in the form of a hysterothecium with separately developed base and cover. Hymenium consisting of both asci and paraphyses. Asci clavate and long stalked. Ascospores elongated, non-septate, hyaline, one-third to one-half the length of the ascus, incased in a hyline, gelatinous matrix. Paraphyses filamentous, hyaline, gelatinously united above the asci into an epithecium.

Type species: *Epidermella communis* (Fries).

Epidermella communis (Fries) n. comb.

Hypoderma virgultorum De Candole, Flore Française, vol. 5, p. 165, 1815, in part.
Hysterium commune Fries, Systema Mycologicum, vol. 2, p. 589. 1823.
Hypoderma commune Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 53. 1861.

Hysterothecia dull black, scattered in light stramineous, oval spots 2 to several mm. long, elliptical, up to 1 mm. long by 650 μ wide, subcuticular. Labia distinct, thickened, tending to become heavily carbonized in the middle region, up to 85 μ wide, bordered inwardly by a bright orange mass of gelatinous, clavately expanded, periphyses 20-25 μ long by 6 μ wide at the tips. Basal layer a plate one cell thick of loose, brown, radiately disposed prosenchyma; this overlaid to a depth of 15-20 μ by a closely interwoven hyaline plectenchyma from which the hymenium arises. Cover a brown, translucent plate of heavily chytinized, aliform mycelium underlaid by several layers of brown pseudoparenchyma, thickest near the labia, very thin at the margins. Paraphyses hyaline, filamen-

tous, nonseptate, simple, not clavately expanded but crushed and bent by pressure at the tips and united above the asci in a gelatinous, orange epithecium about 10 μ thick, 80-125 μ long, about 1 μ wide. Asci clavate, broadly rounded above, tapered to a long, fine stipe, 65–120 μ long, 12–17 μ wide, 8-spored. Ascospores hyaline, cylindrical, nonseptate in the ascus, loosely fasciculate, 20-33 μ long, 3-4 μ wide, incased in a hyaline gelatinous matrix up to 2 μ thick.

Imperfect stage: Leptostroma omissum Hilitzer, Vědecké spisy vydáv. Českoslov. Akad. Zeměd. 3 : 105. 1929.

Type locality: Not given by Fries.

Type specimen: Not cited by Fries. The description is written from Roumeguère's Fungi Gallici exsiccati No. 3546, bearing the note: "sur les sarments dessechees du Houblon, aux environs d'Audenarde (Belgique). (Reliq. Westendorpii)." This is probably the type of Westendorp's f. *Lupuli.*

Notes: The basal plate of the hysterothecium appears to have been produced by the emanation of hyphae from a point located at about the center of the mature hysterothecium. Here, there are as many as 4 polygonal cells from which develop radiating branches whose outward growth takes place by the dichotomous branching of apical cells typical of aliform mycelium. The method by which the outer layer of the cover is produced was not observable; but this layer consists of a densely laid plate of aliform cells, the general orientation of which indicates a development progressing step by step with the basal layer.

The aliform structure of the hysterothecium, together with its subcuticular position and the separation of base and cover, indicates for this fungus a relationship with the Hemisphaeriales as clear cut as is the case with species of Lophodermium.

The material on Cassia, distributed in Ravenel's Fungi Americani exsiccati No. 323, is in our copy sterile but agrees with the Roumeguère exsiccatum in being subcuticular and having an aliform structure.

3. *Epidermella Lauri* (Fries) n. comb.

Hysterium Lauri Fries, Linnaea 5 : 552. 1830.
Hypoderma Lauri Duby, Mém. Soc. Phys. et Hist. Nat. Genève 16 : 55. 1861.
Lophodermium Lauri Rehm, Rabenhorst's Kryptogamen-Flora 3 : 37. 1887.

Hysterothecia gray or dull black, amphigenous in light stramineous spots of variable extent which are sharply delimited by black, stromatic lines, narrowly oblong with rounded ends, 720-3500 μ long, 350-475 μ wide, simple or confluent end-to-end or appearing branched because of lateral confluences, subcuticular. Labia fine and narrow, 15–20 μ wide, only slightly carbonized, reaching to within 200 μ of each end of the

hysterothecium, lined inwardly by a white mass of hyaline, clavately expanded, gelatinous and soon evanescent periphyses 10–20 μ long by 1–1.5 μ wide. Basal·layer a brown, translucent plate of radiately disposed aliform prosenchyma; this overlaid to a depth of 10 μ by a finely interwoven, hyaline plectenchyma from which the hymenium arises. Cover well arched, brown and more or less translucent, consisting of an outer plate of heavily chytinized, radiately disposed aliform hyphae and 2-5 layers of slightly carbonized pseudocollenchyma. Paraphyses filiform, hyaline, nonseptate, simple, not clavately expanded but more or less crushed or bent by pressure and gelatinously fused above the asci to form a white epithecium up to 20 μ thick, 80-100 μ long by about 1 μ wide. Asci clavate to fusiform, rounded above, tapered below to a long thin stipe, 70–80 μ long, 6–10 μ wide, 8-spored. Ascospores cylindrical, hyaline, nonseptate in the ascus, more or less fasciculate and tending to be arranged in pairs in the expanded upper portion of the ascus, 18–30 μ long, 1–1.5 μ wide, incased in a hyaline gelatinous matrix 1–1.5 μ thick.

Imperfect stage: Unknown.

Type locality: Not given by Fries.

Type specimen: Not cited by Fries. The description above is written from de Thuemen's Mycotheca universalis No. 1464.

Host: *Laurus nobilis:* Austria (Jaap, 1916), France (Duby, 1861), Italy (Rabenhorst, exs.), Spain (Duby, 1861).

Exsiccati: Jaap, Fungi sel. exs. No. 559; Rabenhorst, Fungi europ. Nos. 653, 1843; de Thuemen, Mycoth. univ. No. 1464.

Notes: There are two types of mycelium produced by this fungus. One is subcuticular, brown, distantly septate, 3–3.5 μ wide, with a tendency to follow the lateral walls of the epidermal cells and to form, thereby, a loose, subcuticular, extensive network. The other is internal, hyaline, 1–1.5 μ wide and tends to ramify through the host tissues and to collect as a loose subiculum about the base of the hysterothecium.

Duby (1861) considered this a species referrable to his genus Hypoderma, but Rehm (1887) transferred it to Lophodermium, on the basis that the ascospores are acicular and one-celled, though he noted that so far as the ascus shape is concerned it might well be a Hypoderma. Darker, (1932, p. 15) has defined Hypoderma in his key as having one-celled spores, though his figures (pl. 7, figs. 3, 4, 5, 8; pl. 8, fig. 3; pl. 9, fig. 6) indicate that, at least at the time of germination, the spores of pinicole species become two-celled. Partly on the basis of spore length, partly on the basis of spores being or becoming 2-celled in the ascus, he has segregated (*l. c.,* p. 62) *Hypoderma deformans* Weir in a new genus, Elytroderma. A comparison of Rehm's figures of *Hypoderma Rubi* (1887, p. 29, figs. 1–7), as well as examination of other extant material,

indicates that Darker's Elytroderma is more nearly in accord with Hypoderma than are the several pinicole species of Hypoderma recognized by Darker.

The exact definition of Hypoderma rests, however, on the description and figures given by de Notaris (1847), for which the type is *H. Rubi.* Rehm appears to have been right in excluding *H. Lauri;* but his placement of it in Lophodermium is incorrect.

Its position is subcuticular, with relation to its host tissues, and the definitely radiate construction, the presence of aliform mycelium, the separate development of the hysterothecial base and cover, and the presence of periphyses within the ostiole appear to justify the segregation of it in a new genus, along with other similar species.

In the same category belongs the *Hypoderma virgultorum* DC. on the petioles of fallen leaves of Ailanthus and of *Aralia spinosa* distributed in Ellis and Everhart's North American Fungi No. 2378.

4. LOCELLIDERMA new genus

Genus of the Hypodermatacene. Ascomata in the form of hysterothecia, ellipitical to linear, opening by an elongated ostiole bordered by thickened, more or less carbonized labia and lined with gelatinizing, persistent or evanescent periphyses, divided internally into locules by the proliferation of imperfect cross-partitions of pseudoparenchyma from the basal layer, base and cover separate in origin as in maturity. Hymenium consisting of both asci and paraphyses, discontinuous. Paraphyses hyaline, filiform, simple, fused above the asci in an epithecium. Asci cylindrical, 8-spored. Ascospores elongate, 1-septate, hyaline, incased in a hyaline gelatinous matrix.

Locelliderma Ampelodesmi (de Cesati) n. comb.

Hypoderma Ampelodesmi de Cesati, Hedwigia 21 : 8. 1882 and Rabenhorst's Fungi Europaei et extraeuropaei exsiccati No. 2643b. 1881.

Hysterothecia dull to shining black, subepidermal, linear, 1-4 mm. long or by confluence becoming 10 mm. long, 250-500 μ wide, loculate within, divided on each side of the ostiole into subspherical chambers by dark brown, pseudoparenchymatous partitions, the locules 110-150 μ in diameter. Labia indefinite, narrow, carbonized, lined with very short, hyaline, evanescent periphyses. Basal layer a plate one to two cells thick, consisting of brown, translucent pseudoparenchyma; this overlaid to a depth of 15 μ by a closely interwoven, hyaline plectenchyma that is interrupted at the locule walls. Cover dark brown, hardly translucent, pseudoparenchymatous, involving the epidermal cells. Paraphyses hyaline,

filamentous, straight or flexuous, not clavately expanded but bent and crushed at the tips, exceeding the asci by 5-10 μ and gelatinously fused into a thin white epithecium, about 1 μ wide. Asci clavate to subcylindrical or saccate; bluntly rounded above, tapered to a short or long, fine stipe, 65-90 μ long, 12-15 μ wide, 8-spored. Ascospores hyaline, elongated, with rounded ends, straight or somewhat curved, 1-septate, the septum located 3-6 μ from one end and dividing the spore into 2 unequal cells, the spores arranged in 1 or 2 series, each inclosed in a hyaline, gelatinous matrix 2 μ thick, 20-24 μ long, 6.5-9 μ wide.

Imperfect form: Unknown.

Type locality: "Neapolitano, in H. B. (Catanensibus)."

Type specimen: Rabenhorst, Fungi europ. No. 2643b.

Host: *Ampelodesmus tenax:* Italy (Rabenhorst, exs.).

Note: It has seemed impossible to retain this species in Hypoderma, in view of the loculate condition of the hysterothecium and the special manner in which the ascospores are divided by the septum. The hysterothecium, in its loculate character, shows some relationship to the Phyllachoraceae, to which group it would undoubtedly be referred were it not for the fact that the entire "stroma" splits lengthwise in characteristic hysteriaceous fashion; and since it bears along this slit the periphyses characteristic of the Hypodermataceae, it has deserved the establishment of a genus on the basis of its characters.

In crushed preparations, the asci issue from the hysterothecia in subspherical bunches, conforming to the shape of the locules from which they are forced.

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PLATES

PLATE I

FIG. 1.—Surface view of a typical hysterothecium, showing the general shape, the heavily carbonized labia surrounding the slit-like ostiole, the periphyses on the inner edges of the labia, the partially exposed hymenium, and dark hyphae in the epidermal cells of the host. (*Dermascia Festucae,* Roumeguère, Fungi. sel. exs. No. 7143.)

FIG. 2.—Vertical, transverse section of a subepidermal hysterothecium, showing base, cover, subhymenial plectenchyma, hymenium, epithecium, carbonized labia, periphyses, and destruction and involvment of host cells. (*Lophodermium arundinaceum,* Sydow, Mycoth. Germ. No. 1172.)

FIG. 3.—Vertical, transverse section of an immature intraepidermal hysterothecium, showing plectenchymatic base, carbonized cover, and thickened labia, noncarbonized cells of the "slit band," hymenium, and relation to host tissues. (*Lophodermellina pinastri* on Picea, Roumeguère, Fungi Gall. exs. No. 1661.)

FIG. 4.—Median vertical, transverse section of a subcuticular hysterothecium, showing base, cover, carbonized labia, periphyses, hymenium, subhymenial plectenchyma, and relation to host tissues. (*Lophodermina mdcularis,* de Thuemen, Mycoth. univ. No. 75.)

FIG. 5.—Vertical, transverse section near one end of a subcuticular hysterothecium, showing the labia and periphyses as structures distinct from the base and hymenium. (*Lophodermina macularis,* de Thuemen, Mycoth. univ. No. 75.)

FIG. 6.—An ascus and paraphyses, showing the general shape of the ascus, the arrangement of the filiform spores in fascicle and in pairs, and filamentous paraphyses with clavately expanded tips. (*Lophodermina juniperina,* Sydow, Mycoth. Germ. No. 1600.)

FIG. 7.—Distal portion of an ascus, showing the asymmetrically conical apex, the arrangement of spores in pairs, and the tendency of the spores to become coiled. (*Lophodermium arundinaceum,* Sydow, Mycoth. Germ. No. 1598.)

FIG. 8.—Vertical section through the cover of a subcuticular hysterothecium, showing the cuticle of the host (a), the outer, aliform plate with the lateral walls of the cells cytinized (b), and the inner pseudocollenchyma (c). (*Lophodermina macularis,* de Thuemen, Mycoth. univ. No. 75.)

FIG. 9.—Meandering aliform mycelium from the aliform cover of a subcuticular hysterothecium. (*Lophodermina autumnale,* type specimen.)

FIG. 10.—Diagrammatic vertical, longitudinal section through a subepidermal hysterothecium showing the lack of continuity between the base and cover at the ends of the hysterothecium. (*Lophodermium arundinaceum,* Mougeot & Nestler, Stirp. Crypt. No. 655.)
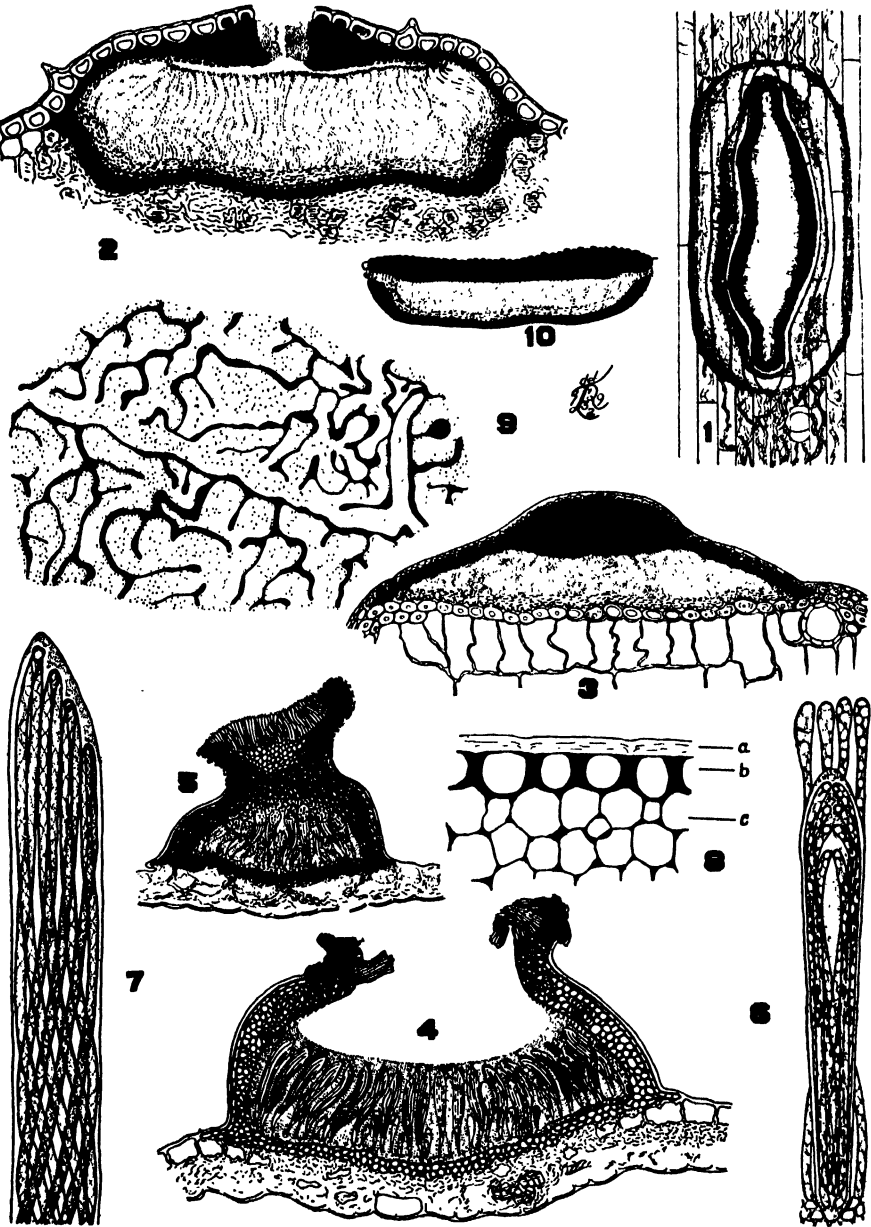
PLATE I

PLATE II

Fig. 1.—Vertical, transverse section through the slit region of a subepidermal hysterothecium, showing the involvement of epidermal cells, the pseudocollenchyma of the cover, the heavily carbonized labia, and the periphyses lining the slit. (*Lophodermium arundinaceum,* Sydow, Mycoth. Germ. No. 1173.)

Fig. 2.—Transverse section of a stoma in an infected leaf of Picea, showing the substomatal stromatic aggregation of fungous cells commonly produced by pinicole species. (*Lophodermellina pinastri,* Roumeguère, Fungi Gall. exs. No. 1661.)

Fig. 3.—Transverse section, through the epidermis, of a leaf of Picea, showing part of the margin of a hysterothecium of *Lophodermellina pinastri.* The two layers of hyphae in the epidermal cells are shown, as is also the manner in which the layers are separated by means of elongated "prop" cells. (Roumeguère, Fungi Gall. exs. No. 1661.)

Fig. 4.—Vertical, transverse section through the margin of a subcuticular hysterothecium, showing (a) the host cuticle, (b) the outer, aliform plate, (c) pseudocollenchymatous cells of the cover, (d) pseudoparenchymatous cells of the cover, (e) pseudoparenchymatic cells of the base, (f) marginal cover cells, (g) hyaline, extra-hysterothecial subicle, and (h) epidermal cells of the host. (*Lophodermina macularis,* de Thuemen, Mycoth. univ. No. 75.)

Fig. 5.—Extra-hysterothecial mycelium of a subepidermal species. The hyphae emanate from the ends of the hysterothecial covers and penetrate the interiors of epidermal cells of the host, where they form a conspicuous network extending some distance from the hysterothecium. (*Lophodermium Dactylis,* Roumeguère, Fungi Gall. exs. No. 1700.)

Fig. 6.—Aliform mycelium from the margin of a subcuticular hysterothecium, showing the indentions in the apical cells which result in dichotomous branching. (*Lophodermina juniperina,* Sydow, Mycoth. Germ. No. 1600.)

Fig. 7.—Aliform mycelium from the margin of a subcuticular hysterothecium, showing the multiple branching of hyphal apices. (*Lophodermina Thuyae,* Davis, Fungi Wisc. exs. No. 114.)

Fig. 8.—Extra-hysterothecial mycelium of a subepidermal species, showing the sympodial branching resulting from the indention, in an aliform manner, of enlarged apical cells of hyphae occupying lumens of epidermal cells of the host. (*Lophodermium Miscanthi,* Baker, Fungi Malayana No. 155.)

Fig. 9.—Habitat sketches of *Lophodermium arundinaceum* on *Phragmites communis.* (a, b. de Thuemen, Mycoth. univ. No. 77; c. Sydow, Mycoth. Germ. No. 1598.)

Fig. 10.—Hysterothecia of *Lophodermium arundinaceum,* much enlarged, on *Phragmites communis.* (de Thuemen, Mycoth. univ. No. 77.)

Fig. 11.—The top of an ascus of *Lophodermium arundinaceum,* showing the acute apex, the pairing of the spores, and the tendency of the spores to become coiled. (Sydow, Mycoth. Germ. No. 1598.)

Fig. 12.—*Lophodermium Brachypodii:* a, habitat sketch; b, c, lateral and top views of a hysterothecium with reflected light; d, hysterothecium by transmitted light. (Migula, Crypt. Germ., Aust. et Helv. exs. No. 240.)
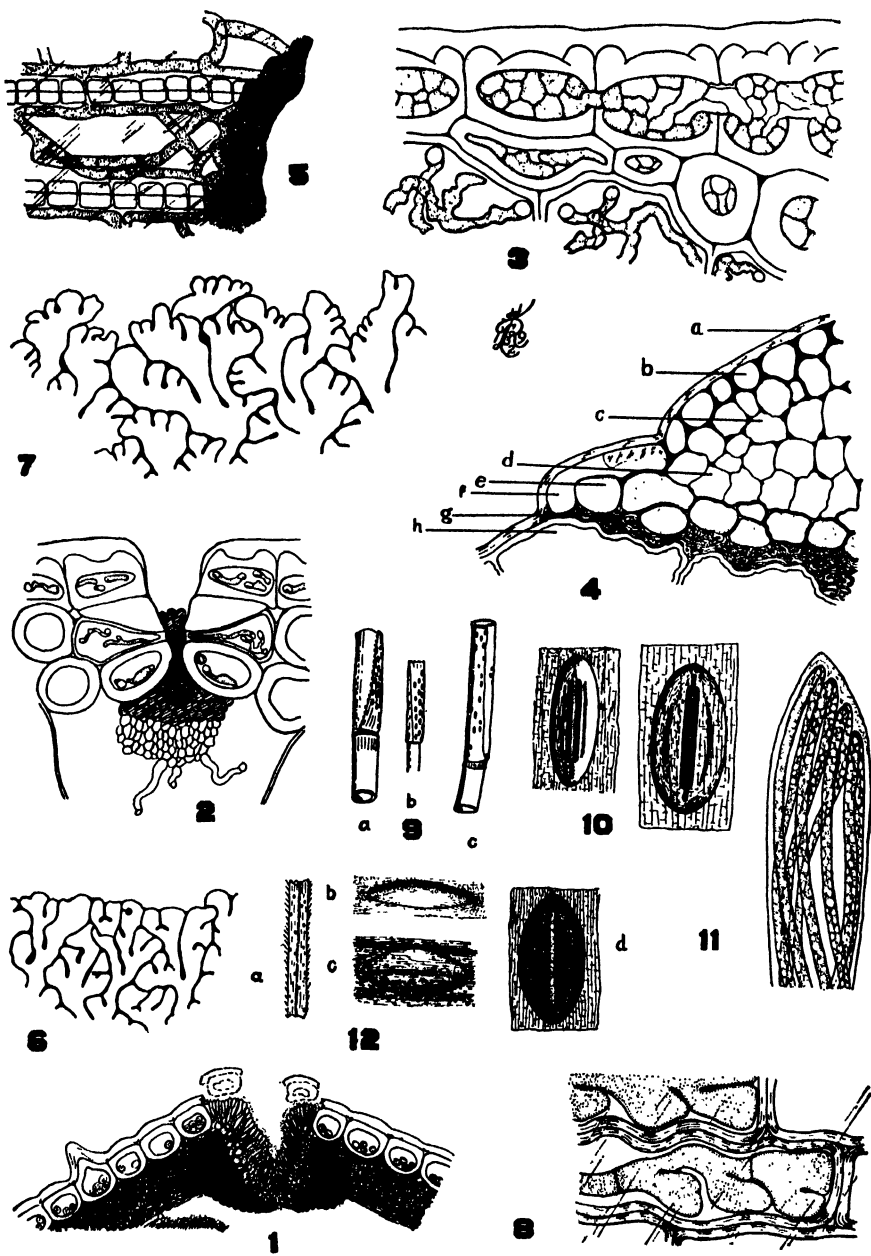
PLATE II

PLATE III

Fig. 1.—*Lophodermium Miscanthi:* Habitat sketch, linear hysterothecium, and ascus with paraphysis. (Baker, Fungi Malayana, No. 155.)

Fig. 2.—*Lophodermium Phlei:* ascus, spores and paraphyses. (Ellis, N. Amer. Fungi. No. 465.)

Fig. 3.—Hysterium of *Dermascia Festucae.* (Roumeguère, Fungi sel. exs. No. 7143.)

Fig. 4.—*Dermascia Festucae:* (a) hysterothecium and (b) tip of an ascus showing coiling of the spores. (Roumeguère, Fungi sel. exs. No. 7143.)

Fig. 5.—*Dermascia latispora:* (a) surface view of a hysterothecium, and (b) the peculiar, subaliform mycelium constituting the outer plate of the hysterothecial cover. (Rehm, Ascomyceten No. 775.)

Fig. 6.—*Dermascia latispora:* ascus, spores, and paraphyses. (Rehm, Ascomyceten No. 775.)

Fig. 7.—*Lophodermellina macrospora:* habitat sketch on a needle of Picea, and ascus and spores (Kunze, Fungi sel. exs. No. 374.)

Fig. 8.—*Lophodermellina Passiflorae,* showing the intraepidermal aliform hyphae of the hysterothecial margin. (Baker, Fungi Malayana No. 38.)

Fig. 9.—*Lophodermellina pinastri:* ascus, spores, and paraphyses. (Roumeguère, Fungi Gall. exs. No. 1661.)

Fig. 10.—*Lophodermellina pinastri:* two habitat sketches showing shape and location of hysterothecia, and the stromatic separations between infections. (Roumeguère, Fungi Gall. exs. No. 1661.)

Fig. 11.—*Lophodermellina pinastri:* aliform hyphae from the margin of the hysterothecial cover. (Roumeguère, Fungi Gall. exs. No. 1661.)

Fig. 12.—*Lophodermellina Rhododendri:* intraepidermal aliform mycelium constituting the margin of a hysterothecium. (Ellis and Everhart, Fungi Columb. No. 738.)

Fig. 13.—*Lophodermellina Tritici:* habitat sketch, hysterothecia enlarged, ascus with spores, and clavately enlarged parapysis tip. (Roumeguère, Fungi sel. exs. No. 6144.)

Fig. 14.—*Lophodermina juniperina:* habitat sketches, natural size and enlarged, on *Juniperus communis.* (de Thuemen, Mycoth. univ. No. 76; Sydow, Mycoth. Germ. No. 1600.)
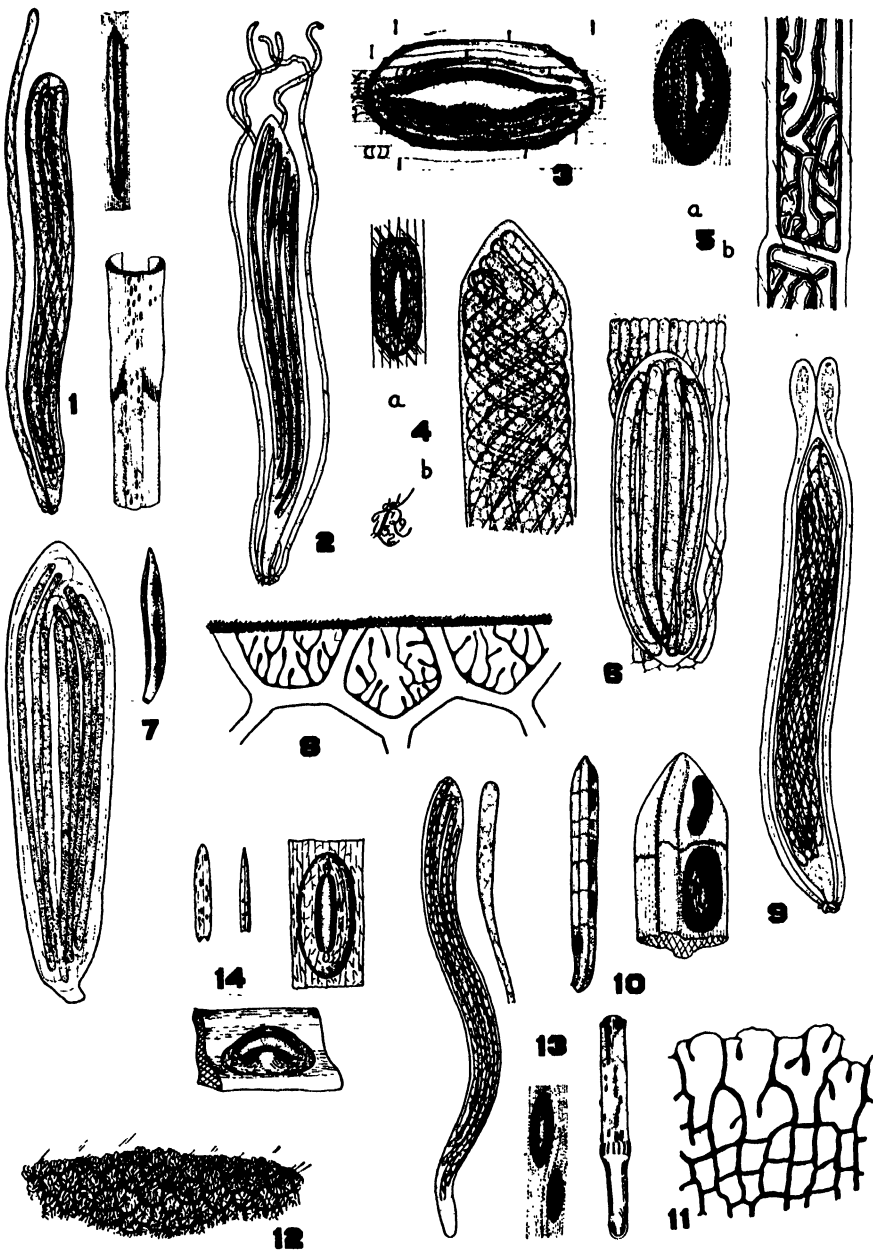
PLATE III

PLATE IV

FIG. 1.—*Lophodermina culmigena:* habitat sketch on *Aira flexuosa,* hysterothecium, and ascus with spores and paraphyses. (Sydow, Mycoth. Germ. No. 1599.)

FIG. 2.—Aliform, meandering mycelium from the cover plate of *Lophodermina culmigena.* (Sydow, Mycoth. Germ. No. 1599.)

FIG. 3.—Aliform hyphal tips from the margin of the hysterothecial cover of *Lophodermina culmigena.* (Sydow, Mycoth. Germ. No. 1599.)

FIG. 4.—Ascogonial cells above the basal plate of a young hysterothecium of *Lophodermina culmigena.* (Sydow, Mycoth. Germ. No. 1599.)

FIG. 5.—*Lophodermina juniperina:* old, empty hysterothecium enlarged, showing subcuticular position and regions of carbonization. (Sydow, Mycoth. Germ. No. 1600.)

FIG. 6.—Dichotomous aliform mycelium from the cover plate of *Lophodermina juniperina.* (Sydow, Mycoth. Germ. No. 1600.)

FIG. 7.—*Lophodermina apiculata:* hysterothecium, enlarged, and ascus with spores and paraphyses. (Kunze, Fungi. sel. exs. No. 372.)

FIG. 8. — *Lophodermina macularis* epiphyllous on *Vaccinium uliginosum:* habitat sketch, hysterothecium enlarged, and aliform hyphal ends from the hysterothecial margin. (Roumeguère, Fungi Gall. exs. No. 553.)

FIG. 9.—*Lophodermina macularis* hypophyllous on *Vaccinium pennsylvanicum:* habitat sketch, hysterothecium enlarged, and aliform hyphal ends from the hysterothecial margin. (de Thuemen, Mycoth. univ. No. 75.)

FIG. 10.—*Lophodermina macularis* hyphophyllous on *Vaccinium uligniosum:* habitat sketch, vertical and lateral views of a hysterothecium enlarged, and aliform cells from the hysterothecial margin. (Sydow, Mycoth. Germ. No. 2146.)

FIG. 11.—*Lophodermina macularis* on "Quaking Ash": habitat sketch, hysterothecium enlarged, and aliform mycelium from the hysterothecial margin. (Ellis, N. Amer. Fungi No. 859.)

FIG. 12—*Lophodermium pinicolum* on *Pinus sylvestris:* distribution of hysterothecia on a needle and separation of individual infections by black, stromatic lines. (Kunze, Fungi sel. exs. No. 371.)

FIG. 13.—*Lophodermina Aleuritis:* habitat sketches, natural size and enlarged. (Baker, Fungi Malayana No. 154.)

FIG. 14.—*Lophodermina Aleuritis:* ascus and spores. (Baker, Fungi Malayana No. 154.)

FIG. 15.—*Lophodermina Aleuritis:* hysterothecium, enlarged showing the extensive subcuticular skirt formed by the aliform mycelium of the hysterothecial cover. (Baker, Fungi Malayana No. 154.)

FIG. 16—*Lophodermium arundinaceum* on *Phragmites communis:* habitat sketch on a leaf sheath, lateral view of a hysterothecium, enlarged, and the tip of an ascus, showing the acute end of the ascus and the tendency of the ascospores to become intricately coiled in the ascus. (Sydow, Mycoth. Germ. No. 1172.)

FIG. 17.—*Lophodermium arundinaceum* on *Phragmites communis:* surface view of a hysterothecium, enlarged, showing the shape of the hysterothecium, its relation to the host epidermis, the shape of the ostiole and of the carbonized labia. (Sydow, Mycoth. Germ. No. 1172.)
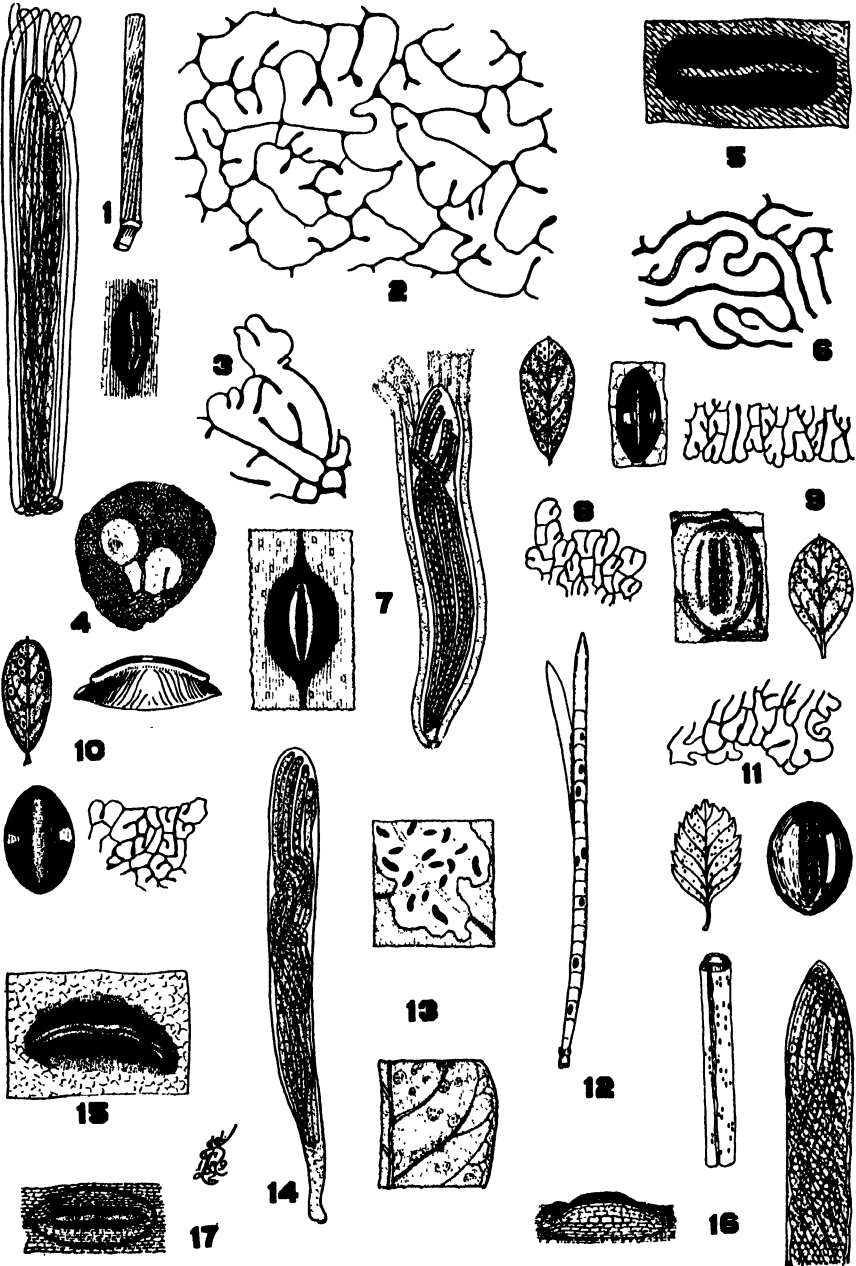
PLATE IV

PLATE V

Type specimen packets of Spegazzinian species of Lophodermium. In his characteristically careful manner, Spegazzini has indicated on the outside of each packet, with notes and drawings, the characters of the hysterothecia and of the asci, paraphyses, and ascospores.

The species illustrated are: 1, *Lophodermium leptothecium;* 2, *L. oxyascum;* 3, *L. subtropicale;* 4, *L. antarcticum;* 5, *L. fuegianum;* 6, *L. clavuligerum.*
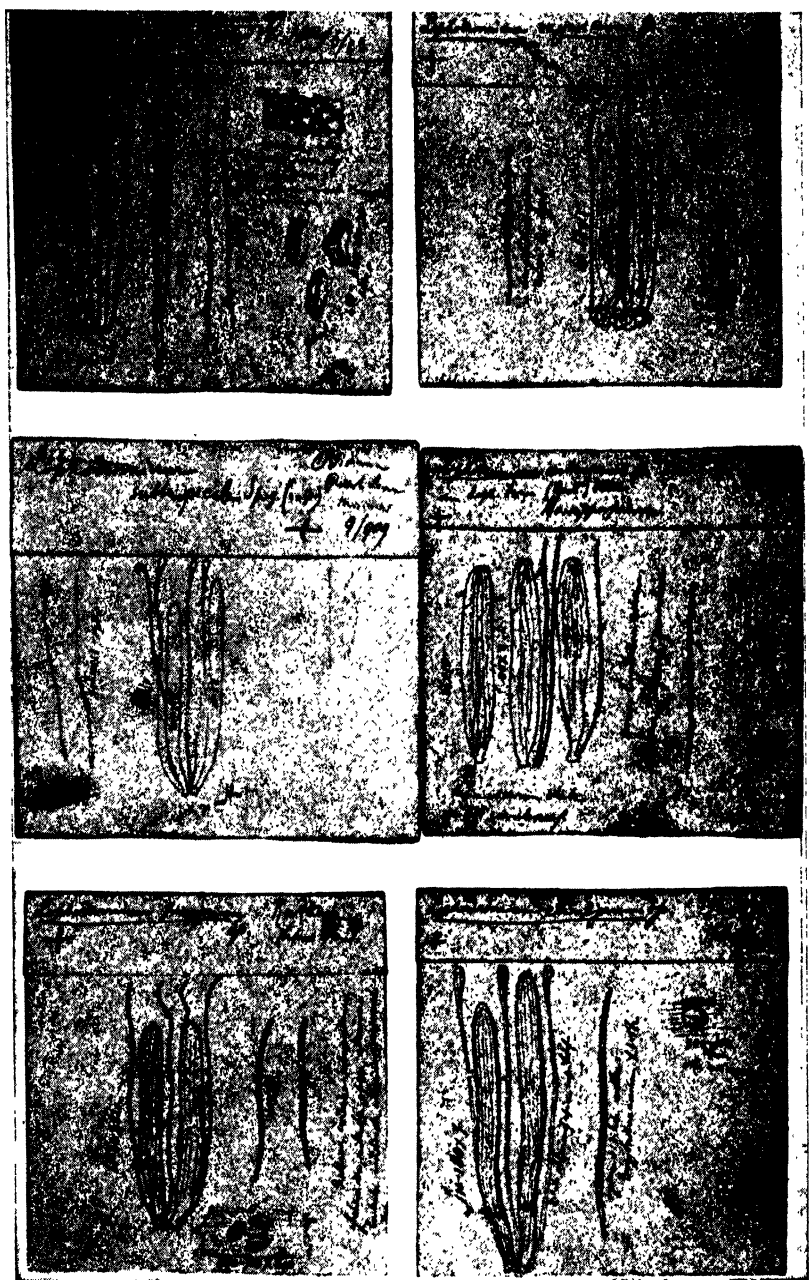
PLATE V

NOTE.—Synonyms are not indicated here, with the exception of a few cases; and these few are set in italics.

Abies alba
    Lophodermellina pinastri, 79
amabilis
    Dermascia consociata, 64
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    Lophodermina uncinata, 111
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    Dermascia lacera, 68
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    Lophodermina autumnalis, 90
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    Hypodermella Abietis-concoloris, 113
    Lophodermellina pinastri, 79
    Lophodermina autumnalis, 90
    Lophodermium Abietis-concoloris, 113
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    Lophodermium decorum, 47
lasiocarpa
    Lophodermellina pinastri, 79
    Lophodermina autumnalis, 90
magnifica
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nobilis
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Acer sp.
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    Lophodermina punctiformis, 107
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    Lophodermina culmigena, 94
Aleurites moluccana
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vulgaris
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    Dermascia rotundata, 72
Carex sp.
    Dermascia caricina, 63
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    Dermascia caricina, 63
glauca
    Dermascia caricina, 63
panicea
    Dermascia caricina, 63

INDEX

NOTE.—For the names of hosts, see the Host List, p. 143. Synonyms are in italics. An asterisk preceding a name indicates a new genus, a new species, or a new combination of names; following a page number, it indicates the technical description of a genus or species.

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  gramineum, 12, 39, 50*
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  infectans, 113
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  javanicum, 115
  juniperinum, 14, 18, 95, 96
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